ORGANIC EVOLUTION

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ORGANIC EVOLUTION

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DEDICATED

TO MY ALMA MATER

RUTGERS UNIVERSITY

PREFACE TO FIRST EDITION

THE addition of another to the long list of books which have been written on evolutionary subjects would hardly be justified in the present instance were it not for the fact that the writer is a paleontologist, whose viewpoint and the evidence at his disposal are therefore materially different from those of the great majority of authors who have enriched the literature of evolutionary biology. The discussion is not based solely upon existing evidences, but also upon the geologic life record, which, although very imperfect compared with that formerly present, is nevertheless wonderfully rich in precept and example such as do not come within the scope of the usual methods of instruction. The work aims to be comprehensive in its scope, but should make a special appeal to students of the past life of our globe. It is hoped, however, that a wider public will learn thereby that the science of Paleontology has a unique social or human value.

The work is the outcome of twenty-three years of college teaching, during the last eleven of which courses more or less closely paralleling the substance of the present volume have been offered to Yale University students. While the course at Yale has been presented in the form of lectures, a text-book, Jordan and Kellogg's *Evolution and Animal Life*, has been used for reference, especially in the earlier lectures. The use of that excellent work has necessarily influenced the author's teaching, and as a consequence the writing of the present book, certain chapters of which will be seen to parallel somewhat those of Jordan and Kellogg. The writer wishes thus to acknowledge his indebtedness to this source. For the larger part of the work, the sources vary, the principal references being given at the close of each chapter. These, collectively, form a representative bibliography of the subject from the present writer's point of view.

Each chapter as it has been written has been referred to one or more of the author's colleagues for criticism, and, so far as possible, such criticisms have been met and suggested additions inserted. It is hoped that by so doing errors of fact have been in a measure eliminated; the final responsibility, however, lies with the author.

I am deeply indebted to my colleagues, Professors Schuchert, Barrell, and Woodruff of Yale University, and to Professor W. K. Gregory of Columbia University and the American Museum of Natural History for painstaking criticism, as they have collectively read and commented upon the entire work. Doctor W. D. Matthew of the American Museum, and Professor H. H. Wilder of Smith College have also aided me in the text, while I am able through the courtesy of President Osborn of the American Museum, the New York Zoölogical Society through Mr. C. W. Beebe, the United States National Museum, that of the Academy of Natural Sciences of Philadelphia, and the Peabody Museum at Yale to present the series of photographs which form the plates. The text-figures, which have been taken from many sources, have, with very few exceptions, been especially drawn for the book, and are very largely the work of Mr. William Baake, which was rendered possible through the generosity of the publishers. A very great portion of the labor of preparing the manuscript and of seeing it through the press has fallen to Miss Clara M. LeVene of the Yale Museum, to whom I am especially grateful.

RICHARD SWANN LULL

YALE UNIVERSITY
June, 1917

PREFACE TO REVISED EDITION

After ten years of service, the Organic Evolution textbook began to show signs of senescence, and need of rejuvenescence was indicated, both as a result of the advancement of our science and of further experience in the presentation of the subject to successive Yale classes. Constructive criticism was invited from a number of my colleagues, and the request was graciously met by Messrs. W. D. Matthew, L. L. Woodruff, G. G. Simpson, C. O. Dunbar, and H. B. Ferris. This criticism has been embodied in the detailed revision and has, I trust, resulted in a further reduction of error and the addition of material of value. One chapter has been omitted, others re-arranged as to sequence, and two new ones dealing with cetaceans and South American mammal radiation inserted. I am indebted to the Bodleian Library of Oxford University and to the British Museum of Natural History for courtesies extended while in residence, during which work on the revision was carried on. I am particularly fortunate in having the direct assistance of Miss Edna M. Gillette and Miss Clara M. LeVene in the preparation of the manuscript and in seeing it through the press.

Richard Swann Lull

New Haven, Conn.
September, 1929

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PART I

INTRODUCTION

CHAPTER I

HISTORY OF EVOLUTION

The problem of the creation resolves itself into two aspects: the origin of the forms of life, and the origin of life itself. It is not surprising, therefore, that these great questions should be among the earliest recorded speculations of humanity, for life in its varied forms comes so close to personal experience.

Theories of Origin.—Four theories have been advanced to account for the existence of the varied kinds of animals and plants on earth to-day—theories in some respects diametrically opposed to one another, in other respects somewhat in accord. They are:

1. Eternity of Present Conditions.
2. Special Creation or Creationism.
3. Catastrophism with
    a. Repopulation by immigration.
    b. Repopulation by successive creations.
4. Organic Evolution.

Theory of Eternity of Present Conditions

The first theory argues for the unchangeableness of the universe, holding not only that organisms have been unalterable throughout their existence, but that they have always existed and will continue to exist in the same unchanging state throughout eternity. This was apparently the belief of very few authorities, for one finds almost no allusion to it in the literature of science, although Hutton wrote: "The result of this physical enquiry is that we find no vestige of a beginning—no prospect of an end." Whether this should be interpreted as a statement that the world has neither beginning nor end is, however, open to question.

Theory of Special Creation

The second theory, that of Special Creation, or Creationism, is the literal interpretation of the Mosaic account of creation set forth in the first chapter of Genesis—a simple story, beautifully told, derived from the Hebrew tradition and well suited to the

state of knowledge of the times and of the people for whom it was written. This account, strictly interpreted, has been the teaching, not alone of the Hebrew, but of the Christian church authorities for many centuries, although the increase of zoölogical knowledge made it harder and harder to reconcile with observed facts, until it was replaced by the doctrine of Evolution.

Suarez.—One of the greatest advocates of the Special Creation doctrine during Christian times was Father Suarez (1548–1617), a Spanish Jesuit priest, who taught emphatically that "the world was made in six natural days. On the first of these days the *materia prima* was made out of nothing, to receive afterwards those 'substantial forms' which moulded it into the universe of things; on the third day, the ancestors of all living plants suddenly came into being, full-grown, perfect, and possessed of all the properties which now distinguish them; while, on the fifth and sixth days, the ancestors of all existing animals were similarly caused to exist in their complete and perfect state, by the infusion of their appropriate material substantial forms into the matter which had already been created. Finally, on the sixth day, the *anima rationalis*—that rational and immortal substantial form which is peculiar to man—was created out of nothing, and 'breathed into' a mass of matter which, till then, was mere dust of the earth, and so man arose. But the species man was represented by a solitary male individual, until the Creator took out one of his ribs and fashioned it into a female" (Huxley).

So profound was Suarez' influence upon European Catholic thought that his teaching continued to be the only orthodox belief in Europe until the middle of the nineteenth century. In a similar manner John Milton (1608–1674) influenced Protestant thought in England by the wondrously written story of the creation in *Paradise Lost.*

Some advocates of the theory claimed that none of the forms had changed in the several thousand years which had elapsed since the beginning; but that the latter-day descendants were in every way precisely similar to the original pair when they issued from the hands of their Creator. Other keen observers, like Linnæus, thought that all the species of one genus constituted at the creation but one form, *ab initio unam constituerint speciem;* their number being subsequently increased through intercrossing with other species, and the hybrids thus produced forming additional

species to those originally created. Linnæus also held that certain forms had lost their pristine character through degeneracy—the result of climate and environment.

Theory of Catastrophism

Cuvier.—A new complication arose through the discovery of older faunas, the remains of which were preserved in the form of fossils and which seemed to represent creatures whose existence antedated that of the living types. Cuvier (1769–1832), one of the founders of the science of Paleontology, became interested in the bones which lay buried in the gypsum quarries in the hill of Montmartre within the present limits of the city of Paris. His studies of these forms, and especially his reconstructions of their skeletons, showed the great anatomist that he was dealing with extinct animals which had no existing representatives. Cuvier also had, because of his official position in the Jardin des Plantes, the opportunity to study hosts of specimens from all parts of the earth, and as a result of his research, gave to the world a new theory, that of Catastrophism or Cataclysm, to account for the extinction of these forms. He is generally accredited with the belief that the cataclysms were world-wide and that the slaughter of the older fauna necessitated the creation of a new one to take its place. That belief, however, was held by later scholars of the same school, but apparently not by Cuvier.

What Cuvier believed was that the catastrophes were local, "sudden revolutions, such as subsidences of the earth's crust, followed by invasions by the sea of continents once dry;" while "other revolutions resulting in the upheaval of mountain chains have again cast back the waters and allowed, on the foundation of the dried bottom of the sea, the constitution of continental soils favorable to the expansion of new terrestrial faunas; these new faunas are not created on the spot, but come from distant regions, their migration from which has become possible owing to temporary bridges between continents" (Depéret). Cuvier's belief has a great deal of truth in it, except that the "revolutions," with resulting climatic change and consequent extinctions and immigrations, have been rapid only in proportion to the length of geologic time, but very, very slow as mortals note the flight of years.

D'Orbigny.—Further knowledge of historical geology led to an expansion of the catastrophic belief far beyond the teaching of

Cuvier, and postulated a re-creation following each cataclysm and corresponding to the principal geologic periods. Alcide d'Orbigny (1802–1857), writing in the year 1848, expounded this theory as follows:

"The first creation shows itself in the Silurian stage. After its annihilation through some geological cause or other, a second creation took place a considerable time after in the Devonian stage, and, twenty-seven times in succession, *distinct creations* have come to re-people the whole earth with its plants and animals after each of the geological disturbances which destroyed everything in living nature. Such is the fact, certain but incomprehensible, which we confine ourselves to stating, without endeavoring to solve the superhuman mystery which envelops it" (Depéret).

Theory of Organic Evolution

Evolution is the gradual development from the simple unorganized condition of primal matter to the complex structure of the physical universe; and in like manner, from the beginning of organic life on the habitable planet, a gradual unfolding and branching out into all the varied forms of beings which constitute the animal and plant kingdoms. The first is called Inorganic, the last Organic Evolution, or descent with modification.

Early Greek Theories.—Organic Evolution is often imagined to be a nineteenth century contribution to biologic science, whereas the idea is itself the product of an evolution of thought and is the fruition of no fewer than twenty-four centuries of speculation and research. The germ of the evolutionary idea had its inception with the Greeks, whose wonderful fertility of mind has so enriched the world, the first writer to deal with the problem, Anaximander, living five and a half centuries before the Christian era. Empedocles (495–435 B.C.) may be called the father of Evolution, though the Evolution that he taught implied no succession of related animals, gradually improving in successive generations, but a series of attempts on the part of nature to produce more perfect forms, the unfit being eliminated. He is the first to show the possibility of the origin of the fittest forms through chance rather than through design.

Another Greek, Democritus (460–?357 B.C.), went further than Empedocles in that he taught the adaptations of single structures and organs, whereas the latter applied the idea to entire organisms.

But by far the most notable figure in Greek philosophy was Aristotle (384–322 B.C.), whose versatility as a writer upon all aspects of human knowledge was remarkable. In view of the limited opportunities for observation possible in those days when the teeming host of microscopic forms as well as the extinct creatures were utterly unknown, the deductions of Aristotle, even where he appears to retrogress from the truth, are highly logical. He did not believe in Special Creation, nevertheless he postulates an intelligent design as the primary cause of the changes which have been wrought in nature, and the central thought in his evolutionary theory, if such it was, is an *internal perfecting tendency* impelling organisms to greater and greater perfection. As a result of this, he saw a complete gradation in nature from the mineral to the plant, the plant-like animal, the animal with senses and hence locomotor powers, and finally man.

Aristotle considered life a function of the organism, not a separate principle, and had an understanding of adaptations and of heredity, even of the atavistic heredity wherein an ancestral trait reappears in a later descendant after having lain dormant for several generations. Osborn says of him:

Aristotle's argument for "operation of natural law, rather than of chance, in the lifeless and in the living world, is a perfectly logical one, and his consequent rejection of the hypothesis of the Survival of the Fittest, a sound induction from his own limited knowledge of Nature. . . . If he had accepted Empedocles' hypothesis [of the origin of the fittest through chance rather than through design] he would have been the literal prophet of Darwinism."

To summarize, then, the Greeks offered as causes of evolutionary change three explanations:

1. Intelligent design,

2. The operation of natural laws implanted by intelligent design,

3. The operation of natural causes due to laws of chance—no evidence of design, even in origin.

Middle Ages.—And now, for hundreds of years, owing largely to the repressive measures of the church authorities, though some, like Saint Augustine, would have taught otherwise, the progress of the evolutionary idea virtually ceased until the coming of the philosophers Bacon, Descartes, Leibnitz, and Kant, and the naturalists Linnæus, Buffon, Erasmus and Charles Darwin, É. Geof-

froy St.-Hilaire, and Lamarck. The philosophers contributed very materially to the problems of causation, but the real proof of Evolution lay in the facts concerning animate nature which the naturalists gathered and explained.

Linnæus.—Among the great naturalists, Linnæus (1707–1778) was a contributor of facts rather than of theory, for his faith in the origin of species through Special Creation never wavered, except that he believed in the production of post-creation forms by hybridizing or by degeneracy due to climatic change. He was one of the first to put systematic zoölogy on a firm basis and advocated the scheme of double Latin names for each clearly defined species of animal and plant. Linnæus' work, however, proved a great stimulus to the research along evolutionary lines which was carried out by his contemporaries and successors.

Buffon.—First among these was Buffon (1707–1788), a French savant, who, Osborn says, was the "naturalist founder of the modern applied form of the evolution theory." Buffon lived in a time when to express one's views along lines not deemed orthodox by ecclesiastical authority might invite serious annoyance or even persecution, and he was not of the stuff of which martyrs are made. To this may have been due his apparent wavering between Special Creation and Evolution. Then, too, he wrote in such a way that, as he hoped, his ideas would be appreciated by scientists but "beyond the reach of the censor and dilettante." This adds to the difficulty of interpretation, as it requires some reading between the lines to get his real meaning.

Buffon's teaching may be briefly summarized thus: The chief factor in the mutation of species was "the direct influence of environment in the modification of the structure of animals and plants and the conservation of these modifications through heredity." The transmission of these acquired characters, however, is nowhere expressly stated by Buffon, but is certainly implied. Packard tells us that Buffon was not an original investigator, leaving no technical papers nor memoirs, but was a brilliant writer and a popularizer of science. His voluminous works express not only the evolutionary factor which he advanced but ideas on the influence of climate on various races of men, the formation of new varieties of animals through human intervention (artificial selection), and the same results produced by nature through geographical migrations. Thus he understood the significance of isolation, although

he did not expressly state it. Buffon did, however, record his views on the struggle for existence to prevent overcrowding and thus to maintain the balance of nature. Herein he anticipates Malthus, whose work on human population later proved to be so great a stimulus to Darwin and Wallace. Buffon also speaks of the elimination of the least perfected species and the contest between the fecundity of certain species and their constant destruction.

Erasmus Darwin (1731–1802) was a country physician, a naturalist, and a poet of some distinction. He was the grandfather of Charles Darwin, to whom he seems to have transmitted the love of science and desire to know what could be learned concerning the deeper problems of life. Erasmus' direct influence upon his grandson, however, through the medium of his writings, seems to have been slight.

The elder Darwin's theory as to the cause of evolution differed from that of Buffon in that he did not emphasize the influence of the directly acting environment, but believed that modifications spring from within by reactions of the organism, an idea more nearly comparable to that of Lamarck, but going even further than the latter's in being applied to plants as well as to animals. Thus he says: "All animals undergo transformations which are in part produced by their own exertions, in response to pleasures and pains, and many of these acquired forms or propensities are transmitted to their posterity." This is the first time that the factor of the inheritance of acquired modifications is clearly stated.

Erasmus Darwin emphasizes the fierce struggle for existence which, he says, checks the rapid increase of life and thus is beneficial in the end; hence he just misses the idea of survival of the fittest in connection with the struggle for existence.

Doctor Darwin believed that powers of development were implanted within the original organism by the Creator, and that these in turn gave rise to the various adaptations without further divine intervention. He does not, however, believe in the internal perfecting principle of Aristotle but holds that the power of improvement rests with the animal's own efforts and that the result of these efforts upon the creature's body can be transmitted to its offspring.

Two distinctly modern conceptions are attributed to Erasmus Darwin: the statement of the evolution of all forms of life from a single protoplasmic mass, or, as he himself expresses it, from a

single filament, capable of being excited into action by various kinds of stimuli; and the idea of the immensity of time—millions of years—required for the evolution of the organic world.

Lamarck (1744–1829) was one of the most remarkable as well as one of the most pathetic figures in evolutionary history. A man of brilliant attainments, yet because of ideas which failed to meet the approval of the influential Cuvier, and because of his own blindness and poverty, he suffered social ostracism for what he thought to be the truth and only received a tardy appreciation years after his death. The work of Lamarck as a philosophical zoölogist parallels that of Erasmus Darwin so closely that it would almost seem as though the latter must have been the inspiration if not the source of Lamarck's thought. The possibility of this, however, is stoutly denied by Packard, who states emphatically that Lamarck was in no way indebted to Erasmus Darwin for any hints or ideas. Charles Darwin notes the similarity when he says: "It is curious how largely my grandfather, Dr. Erasmus Darwin, anticipated the views and erroneous grounds of opinion of Lamarck."

It is the latter's *Philosophie Zoölogique*, published in 1809, which parallels Erasmus Darwin's *Zoönomia* most closely and contains the final statement of the author upon his evolutionary hypothesis, which was never developed beyond this point.

Lamarck's theory of the evolution of animals was not that change was the result of the direct action of the environment, but that the latter acted on internal structure through the nervous system. Herein he agrees with Erasmus Darwin. The latter went still further, however, since he thought that plants could also react to environmental stimulus through their sensibility. Lamarck, on the other hand, thought that plants were directly influenced by their surrounding conditions, so that, while agreeing with the elder Darwin in regard to animal evolution, his views on that of plants were in accord with those of Buffon. Either theory, however, depending as it does upon the changes wrought upon the *individual*, implies the inheritance of acquired characters, a thing which Lamarck assumed and never tried to prove; and, as we shall see, the whole fabric of his theory rests upon the possibility or impossibility of this one point: whether the new characteristics impressed upon the organism during its lifetime can be transmitted to its young.

Among the notable contributions of Lamarck to the science which concerns itself with living things were the term "Biology" (a word coined simultaneously by Treviranus) whereby that science is now designated; his conception that species vary under changing conditions; the theory of the fundamental unity in the animal kingdom; and the idea of a progressive and perfecting development of animals and plants. This last he says is due to a certain order originally imposed upon nature by its Author, which is manifest in the successive development of life. He denied, however, any idea of a perfecting principle in nature. In diametric opposition to Cuvier's teaching, Lamarck denied all catastrophes in geology or sudden changes in organic life, but was an advocate of the Uniformitarian school, believing in a gradual change without any sharp breaks either in the continuity of terrestrial history or in the evolution of animals and plants. All that is needed to effect any evolutionary change, he held, is matter, space, and time.

Lamarck also gives us the first real conception of the tree of life, or phylogeny. All classifications before his time had been simply a numerical succession of zoölogical groups arranged one above another. In Lamarck's earliest attempt, published in 1802, he uses the vertical scale, which Osborn compares to a fir tree with central stem and radiating branches; but in 1809 he had arrived at the true conception of life as a tree branching from the roots into larger and smaller stems. In a later attempt in 1815 his tree is still branching, and he has realized the apparent isolation of the vertebrates, which present-day authorities are at a loss to connect with their invertebrate ancestry. With the development of his tree of life came the conception of extinction of past races of animals and plants. This Lamarck clearly understood as applied to the lower grades of organisms, but he could not imagine how so perfect a being as a mastodon could possibly become extinct except through the interference of mankind. He thought that as the lower forms evolved into higher or became extinct, they were replaced by the increasing creation of new beings. The persistence of certain primitive types was perplexing, but was explained by the apparent fact that in their own peculiar environment there had been but little change, and changing conditions were a *sine qua non* of evolution.

In summing up Lamarck's work, one must account for the small-

ness of his influence upon evolutionary thought, for he had but a single follower in all France. Locally, Cuvier's prestige and his own blindness, which rendered his retirement necessary, were largely responsible. As Osborn says: "Lamarck, as a naturalist, exhibited exceptional powers of definition and description, while in his philosophical writings upon Evolution, his speculation far outran his observations, and his theory suffered from the absurd illustrations which he brought forward in support of it. . . . His critics spread the impression that he believed animals acquired new organs simply by wishing for them. His really sound speculation in Zoölogy was also injured by his earlier and thoroughly worthless speculation in Chemistry and other branches of science. Another marked defect was, that Lamarck was completely carried away with the belief that his theory of the transmission of acquired characters was adequate to explain all the phenomena. He did not, like his contemporaries, Erasmus Darwin and Goethe, perceive and point out, that certain problems in the origin of adaptations were still left wholly untouched and unsolved. . . . His arguments are, in most cases, not inductive, but deductive, and are frequently found not to support his law, but to postulate it."

Lamarck's place among scientists is not yet really established. He was undoubtedly a naturalist of the first rank, but as an evolutionist, although he later gained, especially in America, a large following, he cannot yet be placed, as the crucial point in his whole theory is still *sub judice.*

É. Geoffroy St.-Hilaire (1772–1844), another Frenchman and a contemporary of Lamarck, was not, however, his follower but rather a disciple of Buffon, going back to the old factor of direct environmental influence as the sole cause of evolution. He anticipated a much later writer, De Vries, by teaching that transmutation, or the change from one species to another, might be by sudden leaps or saltations, a theory which was in direct opposition to Lamarck's belief in the slow deliberation of the process. St.-Hilaire believed, however, that these leaps took place, not in the adult but in the embryo, "here the underlying causes of sudden transformation were profound changes induced in the egg by external influences, accidents as it were, regulated by law." As a result of this belief in evolution *per saltum* it was not necessary to show the existence of intermediate forms, those perplexing "missing links" in the phyletic series, and it also removed the objection

that interbreeding would speedily swamp new characters according to the law of averages, because physiological isolation, which prevents indiscriminate mating, would thus be secured. While St.-Hilaire can with justice be called one of the founders of Evolution, his influence in its development was not as great as that of his contemporaries.

Charles Darwin (1809–1882) is beyond doubt the foremost figure in evolutionary history, not so much for the originality of his ideas, for they had already been largely anticipated by his predecessors, but because of the abundant proof with which his statements were accompanied, proof based upon thousands of careful observations extending over a long term of years. Darwin's wonderful development and application of the inductive method, making theory everywhere subservient to fact, and the clarity and simplicity of his exposition made his arguments irresistible, and accomplished what none of those who went before him could possibly have done—the wide acceptance of his doctrine, not alone by biologists but by thinking men in general. While some of the so-called Darwinian factors, notably that known as sexual selection, are to a large extent discredited in the light of our greater knowledge, the fact that Darwin's work paved the way for the general acceptance of the truth of Evolution puts him at the forefront of the master minds whose contributions to the science made this acceptance possible.

The story of Darwin's life is well known. Born on the twelfth of February, 1809, this emancipator of human minds from the shackles of slavery to tradition saw the light upon the very day that ushered in the life of Abraham Lincoln, the emancipator of human bodies from a no more real physical bondage. Darwin studied first at Edinburgh, but finding medicine unsuited to his tastes, entered Christ's College, Cambridge, as a candidate for the church. His love of nature, however, dominated all other interests, and shortly after graduation an opportunity came to join the ship "Beagle" as naturalist in a voyage of exploration around the world. The five years spent upon this memorable journey, the narrative of which is so admirably set forth in the book *A Naturalist's Voyage around the World*, resulted in the accumulation of the first of Darwin's great series of observations, the final decision to devote his life to zoölogical research, and the beginning of that illness which made him a life-long invalid. This last factor

necessitated a retired life and thus proved of indirect benefit, as it enabled him to accomplish the immense amount of work which he did without being impeded by the distractions of a public career. A brief chronology of Darwin's scientific and literary work, which had for its climax the appearance of the epoch-making *Origin of Species*, is as follows:

1831–1836, Voyage of the "Beagle":

1837, Beginning of the note-book for the collection of facts bearing upon variation in animals and plants;

1838, Read Malthus on population [1] and conceived the idea of natural selection as the result of the struggle for existence;

1842, Allowed himself briefly to set down his views for the first time;

1844, Wrote a more elaborate statement of his progress which sets forth the main arguments which were later developed in the *Origin of Species*. These embraced the three principal factors of his theory: the struggle for existence, variation, and natural selection of those variations which conform with environmental need. He also developed the idea of sexual selection and attached more weight to the influence of external conditions and the inheritance of acquired characters than in the edition of the *Origin of Species* in 1859. This statement, amounting to 230 pages, was set apart together with the sum of £400 to £500 with which to publish it in case of the author's sudden death;

1856, Sent Sir Joseph Hooker, the botanist, his manuscript. He had now abandoned entirely the factors of Buffon and Lamarck and placed the utmost reliance upon the efficiency of natural selection as the prime factor in Evolution;

1858, Received from a young man, Alfred Russel Wallace (1822–1913), a brief essay embodying a theory of Evolution of which, as in Darwin's case, natural selection was the prime factor. And strangely enough, it was again Malthus' essay, read by Wallace twelve years before, which stimulated the conception. At first, Darwin was inclined, out of chivalrous friendship for the young man, to suppress his own laboriously elaborated work and to publish Wallace's to the world. Fortunately the good counsels of his friends Hooker and Lyell prevailed and as a result a joint paper setting forth the views of both authors was read before the Linnæan Society of London, July 1, 1858. Then Darwin set to work to write the *Origin of Species*, which was prepared in a few months and published in 1859.

In the first edition of the book, he takes a somewhat less decided view of the efficacy of natural selection, believing it to have been,

[1] In this essay Malthus shows that "population increases in a geometrical, food in an arithmetical ratio." Hence it follows that some very active agent or agents must be at work to keep down the surplus population; otherwise neither food nor terrestrial space would suffice for their support in a relatively brief period of time.

however, the principal but not the exclusive agent in Evolution. Selection, he says, works upon "chance" variations, but by this he does not mean fortuitous in the modern sense, but occurring according to laws of which we have no knowledge. As a result of his extensive observations upon domestic animals, Darwin gradually receded from his extreme views concerning the efficacy of natural selection and began to lean more and more toward Lamarck's teaching. In 1876 in a letter to Moritz Wagner he says: "When I wrote the *Origin* . . . I could find little good evidence of the direct action of the environment; now there is a large body of evidence, and your case of the Saturnia is one of the most remarkable of which I have heard."

In the sixth edition of the *Origin of Species* in 1880, Darwin gave the final expression of his belief in the following illuminating sentence: "This [modification of species] has been effected chiefly through the natural selection of numerous, successive, slight, favourable variations; aided in an important manner by the inherited effects of the use and disuse of parts [Lamarckian factor]; and in an unimportant manner—that is, in relation to adaptive structures, whether past or present—by the direct action of external conditions [Buffonian factor], and by the variations which seem to us in our ignorance to arise spontaneously."

Owing to Darwin's invalidism and the gentleness of his character, he left to others the championing of his cause, his chief exponent being Thomas Henry Huxley (1825–1895), himself a man of remarkable learning, forcible logic, and one of the great masters of written and spoken English, in every way admirably equipped to fight Darwin's battles for him. Huxley's contribution to Biology is, therefore, not alone his many admirable research productions in recent and fossil anatomy, but his service as an educator of the public in commanding the general acceptance of Darwin's teachings.

Since Darwin's day, Evolution has been more and more generally accepted, until now in the minds of informed, thinking men there is no doubt that it is the only logical way whereby the creation can be interpreted and understood. We are not so sure, however, as to the *modus operandi*, but we may rest assured that the process has been in accordance with great natural laws, some of which are as yet unknown, perhaps unknowable.

"The world has been evolved, not created; it has arisen little

by little from a small beginning, and has increased through the activity of the elemental forces embodied in itself, and so has rather grown than suddenly come into being at an almighty word. What a sublime idea of the infinite might of the great Architect! the Cause of all causes, the Father of all fathers, the Ens entium! For if we could compare the Infinite it would surely require a greater Infinite to cause the causes of effects than to produce the effects themselves.

"All that happens in the world depends on the forces that prevail in it, and results according to law; but where these forces and their substratum, Matter, come from, we know not, and here we have room for faith." (Erasmus Darwin, as interpreted by Weismann.)

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CHAPTER II

CLASSIFICATION OF ORGANISMS

Kinds of Classification.—Animals (or plants) may be grouped together for convenience of study in one of two ways: they may be classified taxonomically (Gr. τάξις, arrangement, and νόμος, law) (zoölogically or botanically), according to actual blood relationships, or from the standpoint of their life conditions. The latter classification may be called bionomic, *i.e.* in accordance with the laws of life. The adaptive response on the part of two unrelated organisms to similar environmental conditions may give rise to convergences, wherein organisms come to resemble each other so closely that they have sometimes been actually classed together. The distinction between convergent and homogeneous (*i.e.* of the same race) organisms is often a matter of extreme difficulty.

When the classification is based upon living organisms only, errors are also apt to occur, for groups of animals which to-day stand entirely isolated are shown to be related when their fossil ancestry is known. Zoölogical classification depends therefore in a measure upon Paleontology or the study of ancient life, while bionomic classification is concerned with existing organisms.

Zoölogical Classification

As in a military organization armies are divided into smaller and smaller subdivisions—brigades, regiments, battalions, and companies—so the organic world is divided into corresponding groups which, while increasing in number, lessen in individual importance as one descends the scale. An understanding of these divisions is necessary to our work.

Kingdoms and Subkingdoms.—The organic world is made up of two types of organisms, animals and plants, the first characterized in general by a more active, sentient life, the others passive, lacking in muscular and nervous systems, almost inert. These two groups of organisms are known as kingdoms, and constitute the first subdivision of the world of life. The kingdoms are in turn

divided into subkingdoms, though here there is some difference of usage. These subkingdoms are comparable in that each is made up of unicellular organisms on the one hand, Protozoa (Gr. πρῶτος, first, and ζῷον, animal) or Protophyta (Gr. πρῶτος, first, and φυτόν, plant) as the case may be, and multicellular organisms on the other. To the latter the zoölogists have given the name Metazoa (Gr. μετά, after, and ζῷον, animal), the term Metaphyta being applied to the plants.

Phyla.—Subkingdoms in turn are divided into phyla or types. Both terms are objectionable, as each has more than one usage, but the term phylum (Gr. φῦλον, race, tribe) is the one in general use in this sense. The Protozoa constitute but one phylum, while of the Metazoa there are at least eleven such groups of forms, as, for instance, the molluscs, arthropods, and vertebrates, each separated from the others by very distinctive characteristics, in that their ground plan of structure differs widely in each case. Thus, the molluscs have a soft, unsegmented body with no trace of locomotor skeleton, while the arthropods and vertebrates are both segmented and possess locomotive hard parts, but with the distinction that in the arthropods the skeleton is external while in the vertebrates it is principally internal, the body being stiffened longitudinally by an axis known as the vertebral column.

Classes and Families.—Phyla are divided into classes, such as the fishes, reptiles, birds, and mammals among vertebrates; and these in turn into families, genera, species, and varieties. Extremists in classification use the prefixes *sub-* or *super-* to signify groups somewhat more or less restricted than the unqualified name would imply; thus, a class may include subclasses and these in turn superfamilies, families, and subfamilies before the genera are reached.

Genera, Species, and Varieties.—The chief object of our study being the origin of species, an adequate conception of a species is necessary. While biologists have not yet succeeded in arriving at a unanimity of opinion as to just what constitutes a species, the general conception of a kind of animal or plant to which a definite name has been given, such as a red fox, timber wolf, coyote, or jackal, just about expresses the idea. A species therefore is a group of individual animals or plants resembling each other very closely, not only in broad features but in minute detail as well. In general they are such as can breed together and produce fertile offspring, which in turn may reproduce. This was Huxley's great test of a

species, but does not always hold true. The two species of camel, *Camelus dromedarius* and *C. bactrianus*, will breed together; and the llama, *Auchenia glama*, will breed with the alpaca, *A. pacos*, and the offspring are fertile. This is also true of several species of deer and of certain of the Bovidæ, such as the zebu, *Bos indicus*, and the gayal, *Bibos frontalis;* furthermore, the result of such a cross was bred to an American buffalo, *Bison americanus*, and pro-

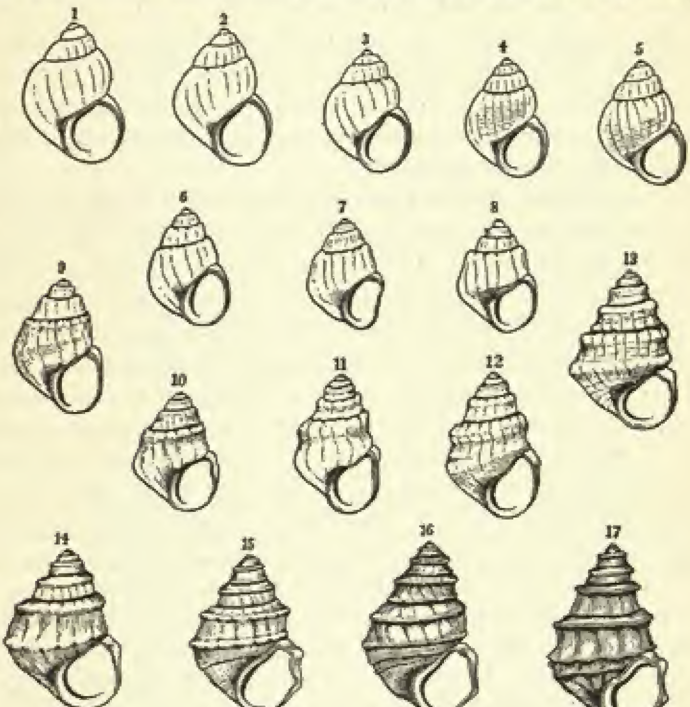

FIG. 1.—Successive forms of *Paludina*, from the Tertiary deposits of Slavonia. (After Neumayr.)

duced a calf, the result of a triple alliance, not only of distinct species, but, according to our present definition, of three distinct genera (Bartlett). Sometimes forms which are quite different, as certain snails (*Paludina*), which might well be considered different species, nevertheless grade into each other if a sufficient series be found and placed in orderly sequence (Fig. 1). Before this series was completed, some six or eight of the then disconnected forms were described as distinct species; but as soon as the con-

necting forms were found, showing progressive modification from the older to the newer strata, the whole were included as varieties of one species (Romanes). Varieties may be arranged in gradational series, each differing from the next in very minute detail. Species do not so intergrade into each other. Were the annectant varieties blotted out by extinction so that only the extremes of the series survived, the latter would then become separate species. Hence one rather poetic definition of species likens them to "islands in a sea of death." All of the dog-like forms which were mentioned by way of illustration, with the exception of the fox, show only specific differences, but any one would at once see a great many important resemblances which seem to imply a very close degree of relationship among them all.

This conception of genera and species was first clearly stated by Linnæus, who gave to each animal and plant with which he was familiar a double name in Latin form, although often derived from the Greek or other languages. These names imply relationship, for the first is that of the genus to which the form belongs, while the second indicates its species. Thus the scientific name of the timber wolf is *Canis lupus*, of the coyote *Canis latrans*, of the jackal *Canis aureus;* but the red fox bears the name *Vulpes vulgaris*, showing it to be not only a separate species but a different genus as well. All of these, however, are dog-like forms and hence belong to the widespread family Canidæ. This family, together with the cats, bears, weasels, and various other animals, is carnivorous, with teeth of a peculiar sort, and to all such forms Linnæus gave the class name Feræ, of which the modern equivalent is Carnivora.

To revert to the definition of species once more, Webster thus defines it: "A more or less permanent group of existing things or beings, associated according to attributes, or properties determined by scientific observation." In general the idea of permanence is implied, but only while conditions remain the same; changing conditions, either through the migration of the animal to a new home or an actual change, climatic or otherwise, in the old one, will react upon the species and thus alter its characteristics. There may also be a gradual change in the organisms in nonessential things in the course of time, even with practically unchanging conditions, especially where isolation of lines is established, as in the case of the various varieties and species of land snails in the radiating valleys in the islands of Tahiti (Crampton).

A species has also been defined as "a stage in the evolution of a race." The species has already been spoken of as an island and the genus may be called an archipelago in a sea of death (Jordan and Kellogg).

Classification of Animals

(Modified from Parker and Haswell)

ANIMAL KINGDOM

Subkingdom PROTOZOA (Gr. πρῶτος, first, and ζῷον, animal). Unicellular, solitary or colonial organisms of minute size, without separate tissues composed of cells.

Phylum I. **Protozoa.** With the characteristics of the subkingdom.

Class I. SARCODINA (Gr. σάρξ, flesh). Without external cell-wall. Locomotor organs pseudopodia. Frequently with a calcareous shell or a siliceous skeleton.

Lobosa (Gr. λοβός, lobe). With blunt or lobe-like pseudopodia. Naked (*Amœba*), or shelled (*Arcella*, etc.). Marine and fresh-water; sometimes parasitic.

Foraminifera (Lat. *foramina*, holes, and *ferre*, to bear). Calcareous shell, generally with numerous fine apertures. Pseudopodia fine, branching or fusing. Marine and fresh-water.

Radiolaria (Lat. *radiare*, to radiate). Siliceous shell, delicate, lace-like. Fine ray-like pseudopodia with central axis. Marine.

Class II. MASTIGOPHORA (Gr. μάστιξ, whip, and φέρειν, to bear). Body with limiting membrane. Locomotion by means of one or more whip-like flagella. Solitary or colonial. Some flagellate forms show certain plant-like characteristics, notably in the presence of chlorophyl, or leaf-green. Thus they are variously claimed by both zoölogists and botanists. Certain members of this group lie upon the frontier between the plant and animal kingdoms.

Class III. SPOROZOA (Gr. σπόρος, seed, and ζῷον, animal). Parasitic Protozoa with complicated life histories. The young are generally reproduced in the form of spores. Locomotor organs usually absent. Many human scourges, such as malaria, are caused by Sporozoa.

Class IV. INFUSORIA (Lat. *infusorium*, because some species are abundant in certain infusions). With limiting membrane. Locomotor organs, when present, numerous hair-like cilia (Ciliata), as in *Paramecium*.

Subkingdom METAZOA (Gr. μετά, after, and ζῷον, animal). Multicellular animals with definite tissues composed of cells, among which there is division of labor. Reproduction by means of ova and spermatozoa (sexual) the rule, although asexual reproduction does occur.

Phylum I. **Porifera** (Lat. *porus*, pore, and *ferre*, to bear). Sponges. Plant-like organisms, motionless, without tentacles. With a more or less complicated internal canal system and with inhalent and exhalent pores. Simple or colonial. In the more complicated sponge stocks the individuals can no longer be distinguished. Skeleton, when present, consisting of

calcareous or siliceous spicules or of chitinous (horny) fibers (spongin), sometimes reinforced by siliceous spicules. Commercial sponges possess a chitinous skeleton without the supporting spicules.

Phylum II. **Cœlenterata** (Gr. κοῖλος, hollow, and ἔντερον, intestine). Hydroids, jellyfishes, coral polyps, etc. Radially symmetrical animals, generally with tentacles and stinging cells. With one internal cavity functioning both for circulation and the digestion of food.

Class I. Hydrozoa (Gr. ὕδωρ, water, and ζῷον, animal). Polyps with a simple internal cavity, either simple (*Hydra*) or forming more or less complex colonies (hydroids) in which there is division of labor among the various individuals (zoöids). The reproductive zoöids take the form of medusoid buds which may become detached from the colony as free-swimming medusæ (Gr. Μέδουσα, Medusa) (jellyfish).

Class II. Scyphozoa (Gr. σκύφος, cup, and ζῷον, animal). Cœlenterates in which the medusæ are large and dominant. There is no hydroid colony, but the medusæ are generally derived from minute polyps known as scyphulæ.

Class III. Anthozoa (Gr. ἄνθος, flower, and ζῷον, animal). Corals. Polyps with complicated internal cavity and with no free-swimming medusæ. They may be either fleshy (sea-anemones) or secrete a horny or calcareous skeleton (corals). Solitary or colonial, the latter sometimes becoming massive coral stocks, aggregates of which form extensive reefs or islands.

Class IV. Ctenophora (Gr. κτείς (κτέν-), comb, and φέρειν, to bear). Comb-jellies. Pelagic cœlenterates which progress by means of rows of comb-like swimming plates formed of fused cilia. More or less ovoid to band-like in shape, and generally provided with two tentacles which bear adhesive, instead of stinging, cells. Never colonial, and exclusively marine.

Phylum III. **Platyhelminthes** (Gr. πλατύς, flat, and ἕλμινς, worm). Flatworms. Bilaterally symmetrical animals, flattened dorso-ventrally, the body cavity filled with a tissue called parenchyma. Digestive and other systems generally much branched. The free-swimming Turbellaria (Lat. *turba*, whirling) have ciliated contractile bodies, while the parasitic forms are not ciliated as adults. Those of the latter which are of simple form are known as Trematodes (Gr. τρηματώδης, having holes), while the elongated, segmented tapeworms, without digestive system, are called Cestoda (Gr. κεστός, girdle).

Phylum IV. **Nemathelminthes** (Gr. νῆμα, thread, and ἕλμινς, worm). Threadworms. Cylindrical, worm-shaped animals with a body cavity. Many are parasitic and may lose the intestinal canal.

Phylum V. **Trochelminthes** (Gr. τροχός, wheel, and ἕλμινς, worm). Rotifers. Variously shaped organisms of minute size, sometimes sedentary, again swimming by means of ciliated bands which may resemble revolving wheels, hence rotifers (Lat. *rota*, wheel, and *ferre*, to bear).

Phylum VI. **Molluscoidea** (Lat. *molluscum*, mollusc, and Gr. εἶδος, form). Lamp-shells and sea-mosses. Attached, bilaterally symmetrical, unsegmented animals, with a crown of ciliated tentacles or spirally rolled arms.

Class I. Bryozoa (Gr. βρύον, moss, and ζῷον, animal) or Polyzoa (Gr. πολύς, many). Sea-mosses. Minute animals usually encased in chitinous tubes or "cells." Generally colonial and often resembling superficially a hydroid or an alga.

Class II. Brachiopoda (Gr. βραχίων, arm, and πούς, foot). Lamp-shells. Marine forms with a bivalve shell, thus resembling the true molluscs (clams and mussels). In the brachiopods, however, the shell valves are dorsal and ventral, whereas in the molluscs they are lateral. The mouth lies between two ciliated spiral arms which rest closely coiled within the shell. Numerous in geologic time, comparatively few living.

Phylum VII. **Echinodermata** (Gr. ἐχῖνος, sea-urchin, and δέρμα, skin). Spiny-skinned animals. Marine, radially symmetrical forms whose parts are in multiples of five. With a calcareous skeleton varying in its development from minute scattered plates to a complete shell. Locomotion by means of a water-vascular or ambulacral (Lat. *ambulacrum*, walk) system which is peculiar to the group. Never parasitic nor colonial.

Class I. Asteroidea (Gr. ἀστήρ, star, and εἶδος, form). Starfishes. With a pentagonal or star-like body formed of a central disc and five (or more) radiating arms.

Class II. Echinoidea (Gr. ἐχῖνος, sea-urchin, and εἶδος, form). Sea-urchins and sand-dollars. Spheroidal, oval, or disc-shaped forms with a solid test or corona beset with numerous spines.

Class III. Holothuroidea (Gr. ὁλοθούριον, zoöphyte, and εἶδος, form). Sea-cucumbers. Oval or worm-like, with leathery body-wall containing minute plates or spicules. A crown of retractile tentacles around the mouth.

Class IV. Crinoidea (Gr. κρίνον, lily, and εἶδος, form). Sea-lilies or feather-stars. Stalked echinoderms, with many-branched arms. Some (Comatula) become secondarily free. Formerly numerous, now relatively rare.

There are two wholly extinct classes, the Cystoidea and Blastoidea, somewhat similar to crinoids.

Phylum VIII. **Annelida** (Lat. *annulus*, ring). Segmented worms. Primitive, worm-like forms, with ring-like or somewhat flattened segments, and without jointed limbs. Marine worms, earthworms, and leeches.

Phylum IX. **Mollusca** (Lat. *mollis*, soft.) Molluscs. Bilaterally symmetrical, unsegmented animals, without locomotor skeleton, but with a more or less developed fold of the body-wall known as the mantle, and a variously formed shell composed chiefly of calcium carbonate.

Class I. Pelecypoda (Gr. πελεκύς, hatchet, and πούς, foot). Bivalves; clams, oysters, mussels, etc. Shell consisting of two lateral valves connected by an elastic hinge ligament. Fixed or free, fresh-water or marine.

Class II. Gastropoda (Gr. γαστήρ, stomach, and πούς, foot). Univalves; snails, etc. With a variously developed and ornamented, generally spirally twisted shell, and an expanded creeping foot. Free-living, salt- and fresh-water, some terrestrial.

Class III. Cephalopoda (Gr. κεφαλή, head, and πούς, foot). Squid, octopus, nautilus, etc. With distinct head which has a circle of arm-like

processes, sometimes bearing tentacles, sometimes hooks or suckers, and the equivalent of the foot of other molluscs. Shell variable; may be absent (octopus), or may be a large, spirally coiled, chambered structure (nautilus) which in some extinct forms was highly complex. Marine. Some of immense size.

Phylum X. **Arthropoda** (Gr. ἄρθρον, joint, and πούς, foot). Arthropods. Bilaterally symmetrical, segmented animals, with jointed appendages. Body encased in an exoskeleton of chitin often more or less hardened by calcareous salts.

Class I. CRUSTACEA (Lat. *crusta*, shell). Crabs, lobsters, and barnacles. Aquatic arthropods, with two pairs of antennæ and numerous appendages. Breathing generally by means of "gills." A few secondarily adapted to terrestrial life. The majority free-living, some fixed or even parasitic.

Class II. MYRIAPODA (Gr. μυρίος, countless, and πούς, foot). Centipedes and millipedes. Numerous similar body segments, each bearing one or two pairs of legs. Air-breathers, some armed with poison fangs.

Class III. HEXAPODA (Gr. ἕξ, six, and πούς, foot). Insecta (Lat. *insectus*, cut up). Insects. Body divided into three distinct regions: head, thorax, and abdomen, of which the second bears three pairs of legs and usually two pairs of wings. The higher insects undergo a complex metamorphosis. This class includes the most highly diversified and by far the most numerous of all animals, except the Protozoa, living under almost every conceivable condition of life.

Class IV. ARACHNIDA (Gr. ἀράχνη, spider). Spiders and scorpions. Exoskeleton chitinous, four pairs of legs. Air-breathers, except the horseshoe crab (*Limulus*), often with silk-spinning and poison glands. Free-living or rarely parasitic, never sedentary.

Phylum XI. **Chordata** (Lat. *chordatus*, having a cord). Chordate animals. Bilaterally symmetrical, generally segmented animals with a perforated pharynx (gill-slits), a hollow, dorsally situated nerve-cord, and an axial, stiffening notochord which is generally replaced by the vertebral column.

Subphylum I. HEMICHORDA (Gr. ἡμι-, half, and χορδή, cord). *Balanoglossus*, etc. Small worm-like animals with rudimentary notochord. Marine. Semi-sedentary.

Subphylum II. TUNICATA (Lat. *tunicatus*, clothed with a tunic). Tunicates or sea-squirts. Generally sedentary marine animals which are free-swimming at least during larval life, when they possess a notochord in the tail. The adult is enclosed in a mantle or "tunic" which may contain cellulose, a substance rarely found in the animal kingdom. Generally with retrogressive metamorphosis.

Subphylum III. VERTEBRATA (Lat. *vertebratus*, jointed).

Section A. CEPHALOCHORDA (Gr. κεφαλή, head, and χορδή, cord). Skull-less, notochord running to end of snout. Blood colorless. Including only the little lancelets, *Amphioxus*, etc., found burrowing in sand near the shore. Nearest the ancestral vertebrate of any living form.

Section B. CRANIATA (Gr. κρανίον, skull). Skull-bearing vertebrates, with red blood.

Class I. *Cyclostomata* (Gr. κύκλος, circle, and στόμα, mouth). Lampreys and hag-fishes. With suctorial mouth armed with chitinous teeth, and no jaws. Elongate, eel-shaped forms, without paired fins.

Class II. *Pisces* (Lat. *piscis*, fish). Fishes. Aquatic, generally scaly or armored, with paired and unpaired fins. Breathing by means of gills, sometimes with accessory lung-like organs. Cold-blooded, usually oviparous (egg-laying) forms.

Elasmobranchii (Gr. ἐλασμός, plate, and βράγχια, gills). Sharks and rays.

Dipnoi (Gr. δι-, doubly, and πνεῖν, to breathe). Lung-fishes.

Ganoidei (Gr. γάνος, brightness, and εἶδος, appearance). Ganoid or armored fishes.

Teleostei (Gr. τέλεος, complete, and ὀστέον, bone). Modern bony fishes.

Class III. *Amphibia* (Gr. ἀμφίβιος, living a double life). Frogs and salamanders. Cold-blooded, naked and slimy or armored, with paired fins transformed into terrestrial hand-like limbs; unpaired fins, when present, never supported by fin rays. Oviparous. Breathing generally by means of gills during larval life and by lungs as adults. With metamorphosis.

Urodela (Gr. οὐρά, tail, and δῆλος, distinct). Salamanders and newts

Anura (Gr. ἀ-, without, and οὐρά, tail). Frogs and toads.

Gymnophiona (Gr. γυμνός, naked, and ὄφις, serpent). Cæcilians, legless, burrowing forms.

Stegocephalia (Gr. στέγη, roof, and κεφαλή, head). Extinct, armored amphibia.

Class IV. *Reptilia* (Lat. *repere*, to crawl). Reptiles. Cold-blooded, scaly or armored, terrestrial or aquatic animals, breathing exclusively by means of lungs. Oviparous, though some snakes and the extinct ichthyosaurs brought forth the young alive (viviparous). The living orders are few:

Squamata (Lat. *squama*, scale). Lizards and snakes.

Chelonia (Gr. χελώνη, turtle). Turtles and tortoises.

Crocodilia (Gr. κροκόδειλος, crocodile). Crocodiles and alligators.

Rhynchocephalia (Gr. ῥύγχος, snout, and κεφαλή, head). An ancient order of which the solitary, lizard-like *Sphenodon* of New Zealand is the sole survivor. Of many extinct orders there are:

Theromorpha (Gr. θηρίον, beast, and μορφή, form). Mammal-like reptiles.

Ichthyosauria (Gr. ἰχθύς, fish, and σαύρα, lizard) and Plesiosauria (Gr. πλησίος, near, and σαύρα, lizard). Marine reptiles.

Dinosauria (Gr. δεινός, terrible, and σαύρα, lizard). Includes small to gigantic terrestrial forms, related to the crocodiles and birds.

Pterosauria (Gr. πτερόν, wing, and σαύρα, lizard). Aërial reptiles with membrane expansions by which they could fly.

Class V. *Aves* (Lat. *avis*, bird). Birds. Warm-blooded, feathered animals, with the fore limbs transformed into wings. Oviparous. A numerous but very uniform class.

Class VI. *Mammalia* (Lat. *mamma*, breast). Mammals. Warm-blooded, hairy forms, generally quadrupedal and terrestrial, some aquatic

(whales, seals), other aërial (bats). The young are with few exceptions viviparously born (alive) and are nourished after birth by the secretions of modified skin (mammary) glands. Chest and abdominal cavities separated by a muscular diaphragm.

Subclass Prototheria (Gr. πρῶτος, first, and θηρίον, beast).

Order Monotremata (Gr. μόνος, single, and τρῆμα, perforation). Egg-laying (oviparous) mammals. *Ornithorhynchus* and *Echidna*.

Subclass Eutheria (Gr. εὖ, well, and θηρίον, beast). Viviparous mammals. Some of the orders are:

Marsupialia (Lat. *marsupium*, pouch). Pouch-bearing mammals. Opossum, kangaroo.

Edentata (Lat. *edentatus*, toothless). Anteaters, sloths, and armadillos.

Insectivora (Lat. *insectum*, insect, and *vorare*, to devour). Shrews, moles, hedgehogs.

Chiroptera (Gr. χείρ, hand, and πτερόν, wing). Bats.

Rodentia (Lat. *rodere*, to gnaw). Rats, hares.

Carnivora (Lat. *caro*, flesh, and *vorare*, to devour). Dogs, cats, bears, seals.

Cetacea (Gr. κῆτος, whale). Whales and dolphins.

Ungulata (Lat. *ungula*, hoof). Hoofed animals, with several suborders. Elephants, horses, rhinoceroses, cattle, deer.

Sirenia (from *Siren*, the manatee). Sea-cows.

Primates (Lat. *primus*, first). Monkeys, apes, man.

Bionomic Classification

This classification of organisms is based upon the mode of life and the consequent adaptive modification of structure, form, and color which in some cases so obscures the fundamental characteristics of the group to which the animal belongs as to make its true classification in the zoölogical scale a matter of great difficulty. For in extreme cases true relationships are betrayed only by studying the life history of the organism and cannot be learned from its adult condition, as in the parasitic barnacle *Sacculina* (see page 234). A bionomic classification, therefore, does not necessarily agree with one based on such revealed relationships, but is, historically, a more primitive classification.

Animals and plants may be considered first in their interrelationships with other organisms and secondly in their relations to the physical environment.

Interrelationships with Other Organisms

Free-living forms are such as are not sedentary nor in permanent association with other organisms in any of the several ways to be described below. They do, of course, depend upon other

animals or upon plants for their sustenance; in the former case they are called carnivorous or predatory, in the latter herbivorous. The predatory animal usually destroys the prey, while the herbivore does not necessarily injure the food plant disastrously. Free-living forms of the same species may band together for mutual aid or defense, when they are called gregarious or communal (see Chapter XVI).

Parasitic (Gr. παρά, beside, and σῖτος, food).—Parasitism will be discussed more at length in a later chapter (Chapter XVII), especially with regard to its degenerating influence upon the parasite. It is an association between one animal or plant and another and while the parasite is benefited in that it obtains food and protection with the least possible effort, the effect upon the host is generally a detrimental one, and sometimes disastrous. But the parasite usually instinctively avoids fatal injury to its host, as that would be decidedly to its own disadvantage unless its days of parasitism be fulfilled. Herein it differs from the predaceous animal, whose association with the prey is transitory, but almost invariably destructive of its life.

Commensal (Lat. *com-*, together, and *mensa*, table) association in contrast with parasitic is mutually beneficial. It does not, however, imply an organic union such as prevails among symbiotic forms, but merely a more or less permanent association for mutual good. The word commensal means *one who eats at the same table*, but in ordinary usage has become obsolete, nevertheless that is what the word implies biologically, *i.e.* an animal which lives with or on another (species), partaking of the same food.

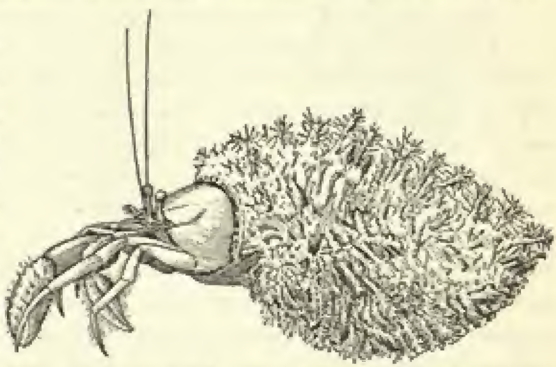

Fig. 2.—Commensal hermit crab, *Eupagurus constans*, and hydroid, *Hydractinia sodalis*. (After Doflein.)

A familiar example is the association of a hermit crab and a hydroid which forms a dense furry growth over the crab's shell.

The crab is a wasteful feeder and the hydroid gathers in the tiny particles of rejected food. It also gets transportation without effort and in return offers the crab a certain immunity from attack, as it is armed with stinging cells and the general appearance of the furry growth renders the crab less conspicuous (see Fig. 2). Another example is the rhinoceros bird which picks ticks from the rhino's back and gives warning of approaching danger to its dull-witted friend. The pilot-fish which accompanies the shark is still another and the peculiar association of gnus, ostriches, and zebras in Africa is a further instance. In the last example it is merely the extension of the mutual aid afforded to the other members of a herd by the sentinels so as to embrace more than one species. The ostrich is so capital a watch-tower that the others have taken advantage of it. Man's association with his domestic animals is a further illustration of the same thing.

Symbiotic (Gr. *σύν*, together, and *βίος*, life). This is the most intimate association of all, again for mutual benefit, and by some writers it seems to be considered as merely a more intimate form of commensalism. Symbiosis means *living together* and in its restricted sense implies an organic union or internal partnership between organisms, so intimate that it can only be severed by death. As thus restricted, it can not exist between two animals but only between an animal and a green, chlorophyl-bearing plant or between a green and a colorless plant, such as show contrasted methods of feeding. The green plant can utilize inorganic compounds, such as carbon dioxide (CO_2) and water, and with the

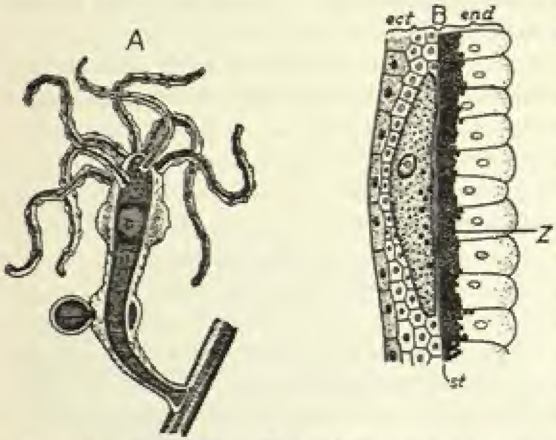

FIG. 3.—Green hydra, *Hydra viridis*, containing symbiotic unicellular plants (zoöchlorellæ). A, entire animal, greatly enlarged. B, section of body-wall: *ect*, ectoderm; *end*, endoderm; *st*, supporting lamellæ; *z*, zoöchlorellæ. (After Weismann.)

aid of sunlight build up starch, liberating some of the oxygen. The animal utilizes the oxygen and organic compounds produced by the plant and in turn gives off the carbon dioxide and certain nitrogenous wastes which the plant utilizes. Thus they are reciprocal. Instances of the first sort are found among the lower animals such as the green hydra (*Hydra viridis*) of which the color is not due to animal pigment but to the presence of numerous minute green plants embedded in its cells (see Fig. 3). Another instance is that of the flagellate protozoön *Euglena viridis* in which precisely the same conditions exist, and many Radiolaria contain symbiotic algæ known as "yellow cells" or zoöxanthellæ. This last relationship is thus described by Thomson:

"They [the 'yellow cells'] are unicellular plants embedded in the transparent living matter of the Radiolarians, and a very profitable partnership has been established. Being possessed of chlorophyl, the Algæ can utilize the carbonic acid formed by the Radiolarian, and are able to build up carbon compounds, such as starch. They give off oxygen, which is of course profitable for the animal, and they doubtless utilize nitrogenous waste products made by the animal. If things are not going well, it is always open to the Radiolarian to digest its partners! The huge numbers of Radiolarians—alike of individuals and of species—seem to indicate that the symbiosis is very profitable."

Symbiotic association of green and colorless plants is found in the lichens, which have been proved to be compound plants, each consisting of "the branching and interlacing threads of a [colorless] Fungus enclosing partner [green] Alga cells. The Fungus fixes the plant, absorbs air, water and salts, protects the Alga from drought and injury, and forms spores which are wafted away by wind and water, and may start new lichens if they find their proper partners. The Alga uses the sunlight to build up carbon compounds, and it joins with the Fungus in forming sexual reproductive bodies. By taking proper precautions the Alga can be got to live in water without the Fungus, and the latter can live on sugary media or the like without the Alga." (Thomson.)

Another remarkable instance of symbiotic association of a somewhat different sort is that of the various beneficial bacteria that live within the bodies of higher animals, especially in the alimentary canal, and which seem to serve a very important function in aiding in the digestion and absorption of food. There is some ques-

tion whether the animal could live its normal life without the aid of these internal organisms. Should their effect be deleterious instead of beneficial, they would be classed as parasites instead of symbiotic partners.

Interrelationships with the Physical Environment

In discussion of the physical environment, the first consideration is the medium in which the organism lives, whether air or water, for this determines its method of breathing. The other features are its relation to the bottom or substratum, and whether or not the creature is a locomotor type, for as we shall see, both of these considerations influence very profoundly the fundamental form and often the color of the organism. The forms which do not depend upon the substratum but are suspended in the medium wherein they live may be either plankton or nekton, according to their locomotor ability. Those which rest or move upon the bottom are called benthos.

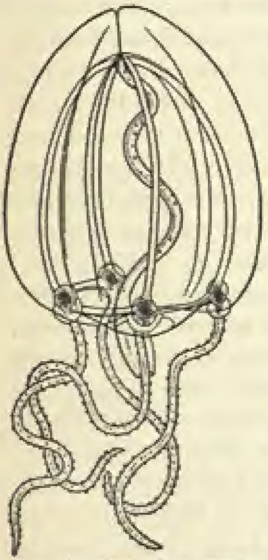

FIG. 4.—Planktonic jellyfish, *Sarsia eximia*. (After Doflein.)

Plankton (Gr. πλαγκτός, wandering) are the animals or plants which float in the water largely at the mercy of wave or current, as they possess little or no locomotive powers other than the ability to rise or sink. They range in size from microscopic dimensions to jellyfish half a yard in diameter, and have in general the following characteristic: Body more or less transparent, usually colorless or pale violet or rose-tinted, though some jellyfish are gaudily colored. The hue is as a rule, however, one which harmonizes well with the water. There is an almost total absence of opaque skeletal structures, only a few possessing delicate calcareous or glassy shells. In general form planktonic organisms are as a rule radially symmetrical, for locomotion in one direction is what usually determines bilateral symmetry (see Fig. 4).

The horizontal distribution of the marine plankton is largely caused by ocean currents which tend to keep the swarms of in-

dividuals together and move them *en masse*. Such powers of locomotion as they possess enable these organisms to sink to greater depths for darkness or tranquillity during stress of weather, coming to the surface at night or in time of calm. During the day many of them sink to a depth of from 50 to 150 fathoms, rising to the surface only on quiet nights.

While marine or halo-plankton (Gr. ἅλς, sea) is the most abundant and varied, fresh-water or limno-plankton (Gr. λίμνη, lake) also exists in nearly all lakes and rivers. Permanent aërial plankton probably does not exist, though microörganisms such as bacteria or "germs" seem to float about in the air almost indefinitely.

Examples of planktonic organisms are the innumerable foraminiferal and radiolarian Protozoa, diatoms among plants, and the swarms of medusæ or jellyfish seen in quiet seas. Many molluscs (pteropods, heteropods) are included, some of which form the staple of diet of the great whalebone whales, and because of their small size are devoured in countless numbers; while the minute shells of Foraminifera, Radiolaria, Pteropoda, and diatoms form the bulk of the oozes which cover thousands of square miles of the ocean floor.

Nekton (Gr. νηκτός, swimming) consists of animals with sufficient locomotive powers to stem the aquatic and aërial currents and go whithersoever they will. Their chief characteristics are well-developed motive organs, spindle form to reduce resistance, bilateral symmetry, body non-transparent, but with distinct coloration which may follow fixed laws (see faunal coloring, sea and air, page 201). The skeleton is opaque and the muscles and generally the organs of special sense are highly developed.

Of marine invertebrates, certain of the cephalopods, notably the squid, are good examples, while among vertebrates the great majority of fishes, sea-turtles, whales, and seals among living types and the great marine reptiles, the ichthyosaurs, plesiosaurs, and mosasaurs among extinct animals, represent the aquatic nekton.

Aërial nekton is abundant in the flying forms, such as insects, birds, pterosaurs, and bats, some of which, notably certain insects and birds, have wonderful powers of sustained flight. Aërial nekton, however, differs from the aquatic in that sooner or later it must come to rest upon the bottom and become benthonic.

Benthos (Gr. βένθος, depths of the sea).—Benthonic forms are the bottom-dwellers, whether fixed to the substratum or with powers of locomotion over it. The former are called sedentary, the latter vagrant benthos. Sedentary benthonic forms, as a rule, exhibit radial symmetry, well shown in corals and crinoids on the part of animals and in the great majority of higher plants. Marked exceptions, as in the brachiopods and barnacles, do occur. Of course this radial symmetry is only attained in its perfection where the environmental conditions are alike on all sides. Among sedentary animals so great a dependence is placed upon food swept within reach by means of stream, tidal, or wave action, that the food-getting organs are apt to degenerate or never develop, and often a special ciliary device takes their place, as in the brachiopods, crinoids, pelecypod molluscs, tunicates, and even in the lancelet (*Amphioxus*) and larval lamprey (cyclostome) among vertebrates. Loss or non-development of musculature, locomotor organs, bilateral symmetry, and organs of special sense are characteristic of sedentary benthos, and with rare exceptions colonial organisms are restricted to this group (see Fig. 5).

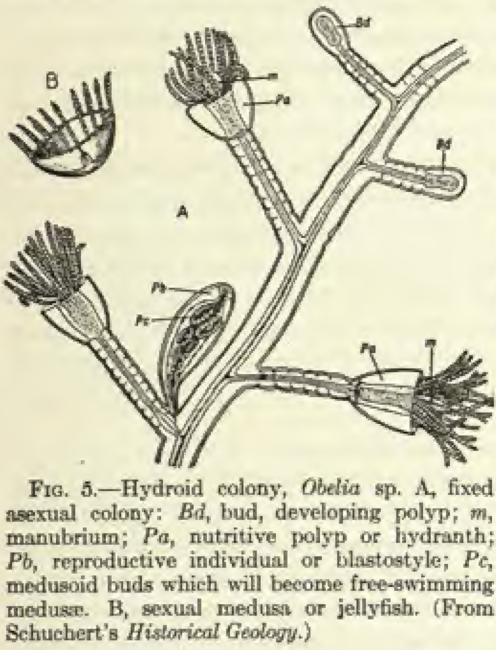

Fig. 5.—Hydroid colony, *Obelia* sp. A, fixed asexual colony: *Bd*, bud, developing polyp; *m*, manubrium; *Pa*, nutritive polyp or hydranth; *Pb*, reproductive individual or blastostyle; *Pc*, medusoid buds which will become free-swimming medusæ. B, sexual medusa or jellyfish. (From Schuchert's *Historical Geology*.)

Examples of *sedentary benthos* would be the sponges; hydroids, with the exception of the remarkable Siphonophora, a free-swimming (planktonic) colony wherein division of labor among the various zoöids has been carried to an extreme; Anthozoa, sea-anemones (see Fig. 6), and corals; Molluscoidea as a whole; barnacles among the Crustacea; certain bivalve molluscs, such as the oysters; and most of the tunicates. With plants, almost all belong

to this category, the only exceptions being the motile bacteria and other Protophyta which have been included under plankton. Nektonic plants are unknown. While aërial sedentary benthos includes the great bulk of the higher plants, air-breathing sedentary animals are rare. A number, which like the barnacles may be left bare by the retreating tide, thus become temporarily aërial but do not respire air, although provision has to be made to withstand the exposure. The only true aërial sedentary benthos seems to be the scale insects (Coccidæ, see Fig. 19) which attach themselves permanently to some plant, twig, leaf, or fruit, and remain constantly in one place thereafter as long as the plant juices yield sufficient nourishment. Drying up of the leaf upon which they live has been known to cause a very short migration, and while extremely degenerate and scale-like, as the name implies, they never wholly lose their organs of locomotion.

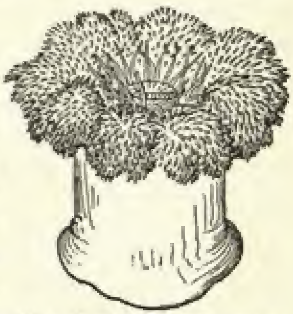

Fig. 6.—Benthonic sedentary anemone, showing radial symmetry. (After Emerton, from Schuchert's *Historical Geology*.)

The group known as *vagrant benthos* is an extremely extensive one, including a large number of marine, but fewer fresh-water types, and almost all air-breathing animals. Bilateral symmetry is the rule, though some, notably the echinoderms, are radially symmetrical. This radial symmetry of the echinoderms masks a more primitive bilateral symmetry, whereas in such forms as the irregular sea-urchins a secondary bilateral symmetry is very marked. Coupled with bilateral symmetry goes the development of locomotor and the higher sense organs, and because of the intensity of the struggle for existence the adaptations of form, color, and food-getting devices are extremely varied. True locomotor colonies, such as the bryozoan *Cristatella*, occur but are very rare, though other animal associations, gregarious or communal, are frequent. The transition from the vagrant benthos to nekton is easy and the instances numerous, and in some cases it is difficult to know under which category the animal should be placed, as in certain marine worms and the sea-otter.

The term *mero-plankton* (Gr. μέρος, part) was introduced by Haeckel to include the free-swimming young of benthonic organ-

isms which lead, during their larval state, a planktonic existence. These forms are as a rule extremely small and have feeble powers of locomotion, generally by means of cilia. Nevertheless they are so numerous that the upper strata of the oceans are literally crowded with them and they form a great source of food supply for the more aggressive forms of life. They pass their short existence floating about in the sea, in swarms. Sooner or later, however, they sink to the bottom, and if they fall upon the proper sort of substratum, they develop into the benthonic adult; but if they fall upon an unfavorable bottom, or if food supply is scarce, they perish.

The necessity of some means of dispersal or for the repopulation of an area wherein accident has destroyed the original inhabitants is imperative, and in sedentary adults can only be attained by this means. Mero-planktonic larvæ are found in every group of aquatic sedentary benthonic animals. The young of the sedentary scale insects, on the other hand, which are active for a brief time, are vagrant benthos. Germs, spores, and many seeds like those of the maple and dandelion constitute about all that can possibly be included in aërial mero-plankton.

Pseudo-plankton (Gr. ψεῦδος, false) is a term proposed for organisms such as the sargassum or gulf sea-weed which is normally or in early life an attached benthonic organism but which becomes planktonic. The meaning of the term has been extended to include plants or animals living as sedentary or vagrant benthos upon floating objects, such as the algæ, hydroids, or bryozoans, which may be attached to the floating sargassum, and the crustaceans, molluscs, or other animals which dwell among them. In many instances the pseudo-planktonic existence of these forms is due to accident, but on the other hand it seems to be habitual with certain forms, which, like the goose-barnacle, *Lepas*, rarely occur except attached to floating objects such as timber or the bottoms of ships, especially when the latter are derelict. Many of the animals found on floating sargassum seem to be characteristic of it in this condition, as they do not occur when it is attached.

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CHAPTER III

GEOGRAPHIC DISTRIBUTION

Kinds of Distribution.—The distribution of life on earth has three aspects, two of which are distributions in space and one in time. Of course every organism can be considered from all three points of view, but a clear comprehension of each can only be obtained by treating them separately and in order.

These three distributions are known as follows:

In space:
Geographic. Horizontal or surficial distribution.
Bathymetric. Vertical or altitudinal distribution.
In time:
Geologic. Durational distribution.

Geographic Distribution.—The distribution of life over the earth's surface is world-wide, as no place is so forbidding as to be entirely without its flora or fauna; the dense tropical forest, the bleakest mountain, the scorching heat and drought of the desert, the devastating cold of the polar regions: each has its quota of inhabitants, living out their lives as best they may.

Closer study, however, reveals the fact that the distribution of life is by no means a uniform one, and, aside from differences in faunas, due to climatic or other causes, there are peculiar instances of isolated distribution. Thus, for example, Africa has elephants, antelopes, and great apes such as the gorilla and chimpanzee in its fauna, while Brazil, with very similar environmental conditions, has none of these, but instead possesses the tapir, sloths, and prehensile-tailed monkeys. The tapirs themselves are found in Central and South America and again in the Malay Peninsula and Sumatra, a curious instance of discontinuous distribution, explicable only by assuming that the American and Malay tapirs are the last survivors of a widespread race, whose intervening representatives have been blotted out.

Again, it is seen that the faunæ of Great Britain and Japan, which are separated by thousands of miles, are very similar,

whereas in Bali and Lombok, two small islands in the Malay Archipelago, separated by a strait only 15 miles wide, the animals are much more unlike.

Thus it is evident that the dispersal and distribution of animals is governed by laws which are far from simple.

To understand them thoroughly "the zoölogist must trace out in detail the exact area or areas inhabited by the several species, genera, and larger groups of animals, and this process to be reliable must be based upon a true and natural classification of the animals themselves. The latter can only be attained by a due consideration of the theory of evolution (or descent with modification) as generally understood at the present day. With this must be intimately associated a knowledge of extinct forms and their distribution in time and space, and this again depends upon an acquaintance with the extent and relative position of the various fossil-bearing strata which build up the huge series of sedimentary rocks" (Bartholomew).

Dispersal of Animals

Necessity.—The struggle for existence brought about by the rapid rate of multiplication of all animals and the consequent scarcity of food within a given area renders the dispersal of animals imperative. Not only is this struggle between members of the same species, but between allied species or any sorts of animals whose needs are sufficiently similar to induce competition. Again, gradually changing climatic conditions, which render the old home no longer suitable, impel migration where migratory roads exist, otherwise gradual extinction is often the result. A study of the distribution of fossil animals such as the elephants or horses (see Chapters XXXV and XXXVI) gives evidence of repeated and world-wide migrations which probably occurred as often as opportunity arose. The extension of geographical range seems, therefore, to be a prime necessity in the great majority of organisms.

Barriers to Dispersal

Topographic Barriers.—Such barriers as high and extensive *mountain ranges* limit the distribution of many terrestrial forms, and in general are more effective if the mountains are more or less parallel with the equator, as in Europe and Asia. Here we find a marked difference between the species occupying the northern and those occupying the southern slopes. This is notably true of the great Himalaya Range in northern India, which rears its

mighty summits far beyond the limits of perpetual snow. On the south we have the hot, moist plains of India, with a very distinct tropical fauna which in many respects resembles that of Africa. North of the barrier, conditions of climate, both in temperature and degree of moisture, are entirely changed, and with them appear animals, with some notable exceptions, of a totally different sort, more nearly comparable to those of Europe. In the New World where the mountain chains in general run north and south, their influence upon animal distribution is vastly less, and in no case do they form striking boundaries between zoögeographical realms (see page 49), as do the Himalayas.

The mountain ranges in the western United States do exert a certain influence, however, principally through their control of humidity. The winds from the Pacific are often laden with moisture, but as they reach the mountain uplift they are deflected higher and become cooler, which causes the precipitation of the moisture in the form of rain. On crossing the barrier, the winds are practically moistureless and, as a consequence, aridity of climate prevails east of the mountains, producing conditions ranging all the way from dry plains to actual desert. This of course has its profound influence upon the character of the vegetation and consequently upon plant-feeding animals and indirectly, though to a less extent, upon carnivores. In North and South America the animals are thus influenced in their range directly by conditions of temperature and rainfall.

One important topographic barrier in North America is that which limits the Mexican plateau and again forms a line of demarcation between faunal realms. The plateau itself, though extending well into the tropics, has a temperate climate, and the fauna is similar to that of the region to the north and northwest. From the edge of the plateau the land drops away abruptly and conditions rapidly change to those of a hot, moist, tropical region, with a corresponding change in the plant and animal life, which is now that of tropical Central and South America.

Climatic Barriers.—While *degree of heat* is of prime importance in limiting animal dispersal, Heilprin thinks that its influence has been largely overestimated. Notable instances in proof of his contention are the tiger and elephants. The former, while its normal home is in the hot districts of India and the Indian archipelago, is not restricted to those regions nor to such as have similar

climates, for it is found "in the elevated regions of the Caucasus and the Altai chain, and in the Himalaya range its footprints are not infrequently found impressed in the fields of snow. It is a permanent inhabitant of the cold plains of Manchuria and the Amoor region . . . prowling about even in winter along the icy margins of the Aral sea." The northern range of the tiger extends to about 53° north latitude, as far north as Lake Baikal in Siberia or Lake Winnipeg in Canada. Elephants likewise do not seem to suffer from cold, provided a sufficient amount of water be obtainable. Hannibal, who invaded Italy in 218 B.C., took a herd of war-elephants, presumably African, over the Little St. Bernard Pass, which has an altitude of 7176 feet. Elephants also range in altitude in the Kilimanjaro region of eastern Africa from sea-level up to 13,000 feet, which must give a marked temperature range; the Indian elephant appears to be equally at home among the cool mountain heights and the hot and jungly lowlands.

The influence of temperature is much more marked in limiting the distribution of cold-blooded animals or those which depend upon external temperatures for the maintenance of their bodily heat, than in the warm-blooded forms. Thus the amphibians and reptiles are tropical and temperate in their distribution, rapidly diminishing in numbers toward either pole. Salamanders are limited to about the sixty-third parallel in Europe, while frogs and toads are absent only from the higher latitudes north and south.

Reptiles, on the other hand, are more restricted; the crocodiles are tropical or subtropical in their distribution, the northern limit of the turtles is 50°, while of the lizards there are few beyond 40°, and at 60° the order entirely disappears. Snakes have the widest range, but only three species in Europe are found beyond 55° and but one, the common viper, extends to the Arctic Circle. The terrestrial vertebrates of the frigid zones are therefore entirely birds and mammals, whose constant temperature and efficient bodily clothing enable them to maintain an active existence where the reptiles and amphibians would be reduced to a condition of torpor. This torpor can be endured for a while and the period of hibernation or winter sleep on the part of temperate cold-blooded animals is a normal manifestation, but it has its limits and can not extend over too great a sum total of the animal's life. The presence of fossil reptiles or amphibia in the rocks of a given geologic period is, therefore, highly indicative of past climatic conditions.

Lack of moisture controls the distribution of animals and plants principally where it is of sufficient extent to produce desert conditions, for while many forms are marvellously adapted to withstand the harshest drought (see Chapter XXIV), for others it forms an insuperable barrier.

The most notable desert barrier is that of the Sahara, which forms the area of demarcation between the Ethiopian or African zoögeographical realm and the Eurasian. So efficient is it that such mobile forms as the deer, which are found in the Americas from the Straits of Magellan to the Arctic and over the entire Eurasian continent except the Arabian peninsula and the adjacent area to the east, are totally absent from Africa except in its extreme northern part, from the Straits of Gibraltar to Tripoli. Of course they are absent from the long isolated Australian region except where they have been introduced by human agency. The Sahara in Africa and the Arabian desert are impassable to such forms. Animals like the Amphibia, which require moisture for their larval life and have no great migratory powers, find even a small arid area an insuperable obstacle.

The *increase of moisture* renders a region unsuitable for certain forms of life, in part due to possible swampy conditions which may make the area impassable to creatures not adapted to them. Swamp-dwelling generally places its mark upon the animal, as in the splay feet of certain Permian reptiles. It is doubtful, however, whether even extended morasses act as a very great barrier to dispersal. Increased humidity does have a marked effect secondarily in affecting the vegetation, the spread of insect life, and the like, to be described below.

Vegetative Barriers.—The profusion of vegetation depends very largely upon the climatic conditions mentioned above—temperature and degree of moisture—and its prevalence is favorable to the dissemination of certain types and unfavorable to others. The influence of vegetation is both direct and indirect—direct in the impossibility of forest-living, especially arboreal animals crossing regions where forestation does not occur; and in forming, especially in the tropics, so dense a growth of jungle that larger terrestrial animals are incapable of penetrating it. Thus, in Pleistocene times mastodons of the genus *Dibelodon* (Chap. XXXV) migrated from North into South America over the newly established isthmian land bridge, but during the Pleistocene, while

there were several species of magnificent elephants (*Elephas* and *Mastodon*) in North America, none of them apparently succeeded in penetrating south of the southern limits of the Mexican plateau. The one possible recorded exception is that apparently of a true elephant (*Elephas columbi*), a tooth of which has been reported from the Lower Pleistocene of Cayenne, French Guiana. What the conditions were which prohibited the passage of the later elephants into South America, while the earlier ones effected a crossing, we do not surely know, but the presence of a tropical jungle too dense to be penetrated by such huge beasts as these is highly suggestive, for at the present day the vegetation is said to be impenetrable to an animal as large as a man, without mechanical aid.

The lack of vegetation very effectively limits the distribution of certain forms, notably the primates, which with few exceptions are dwellers in tropical forests. Not only do they need trees for their safety and usual mode of progression, but also as a source of food, for the primates as an order live upon fruit, nuts, and blossoms, as well as upon insects and small birds, all of which are products of these forests. Primates were very prevalent during the Eocene in western North America. At the close of the Eocene period, however, they became utterly extinct in North America, nor is there the slightest evidence of their reappearance until the coming of man. The Eocene, especially during the middle part, when the primates were most abundant, was a time of subtropical or warm-temperate conditions, as the rocks contain palms and bananas mingled with many similar mild temperate trees. With the ushering in of the next period, however, that of the Oligocene, and more especially in the Miocene, the tropical forests gave way to those consisting largely of deciduous trees which could not support a primate population all the year, hence their local extinction.

This serves to illustrate not only the means whereby the absence of vegetation may limit dispersal, but also the way in which *food supply limits distribution*. Other illustrations would be the necessity for trees and shrubbery for animals with short-crowned browsing teeth, on the one hand, and of extensive pasturage of harsh grasses for those with long-crowned grazing teeth, on the other, each type of vegetation being unadapted to the other type of animal. Vegetation is important also in the case of many insects; caterpillars, for instance, may be addicted to a certain species of

food plant and be coextensive with it in distribution and unable to exist where the plant does not occur. Conversely, some plants are absolutely dependent upon certain species of insects for pollination, without which they can not propagate their seeds. Parasitic insects which depend in turn upon the plant-feeders can not of course exist where the latter do not occur, for many parasites are limited exclusively to a certain genus and species of host, and this again may be restricted to a very small group of plants. Insectivorous birds may be in a measure dependent on certain specific insects, the limits of whose distribution determine theirs, while frugivorous birds, or those which, like the humming-birds, sip nectar from the flowers, are directly limited by the existence of certain types of vegetation. "Thus the whole fauna and flora of a district is bound together by a complicated network of particular conditions, and the slightest alteration in any detail may upset the balance of the whole and lead to far-reaching and unforeseen results" (Bartholomew).

Large Bodies of Water.—Extensive bodies of water, when not frozen, form perhaps the most insuperable barriers of all, especially to terrestrial vertebrates like the amphibians, reptiles, and mammals, but not to those which have powers of sustained flight, such as birds and bats. Fresh-water fishes are also prevented from migration by large bodies of salt water, although certain fishes such as the shad, salmon, sturgeon, and smelt—the anadromous (Gr. ἀνά, up, and δραμεῖν, to run) fishes—pass from salt to fresh water annually, while in the catadromous (Gr. κατά, down) eels the reverse migration occurs. The barrier is effective, therefore, only in the case of exclusively fresh-water types, such as the carps, garpikes, catfishes, bowfin, and brook trout, some of which are quite locally restricted. To the modern Amphibia salt water constitutes a most effective barrier as common salt is poisonous to the amphibia, even a solution of 1 per cent preventing the development of their larvæ.[1] Undoubtedly, however, many individuals have made long voyages across the seas on floating timber (see page 46). Solutions of lime are likewise detrimental to many species, and as a rule limestone-terrain is poor in amphibian life; *Salamandra maculosa*, for instance, is absent in Central Germany on the Muschelkalk, but occurs in abundance in neighboring districts of sandstone or granite (Gadow).

[1] An exception to this is seen in the tadpoles of frogs which have been observed developing in the waters of a tidal creek opening into Manila Bay (see page 61).

Amphibia are, as one would infer, almost completely absent from oceanic islands, the Seychelles, New Caledonia, and the Fiji and Solomon islands forming island groups exceptional to a general rule. Another remarkable fact is the very nearly universal limitation of the tailed forms—sirens, newts, salamanders, etc.—to the northern hemisphere, for the southern land masses, Australia, Africa, and South America, are almost if not entirely isolated by the oceans, and the small migratory roads left open, which have proved sufficient for such creatures as the mammals, are inadequate for these inactive amphibians. The burrowing cæcilians, on the other hand, are confined to South America and Africa, with the exception of the Seychelles, southern India, and the East Indian islands of Sumatra, Java, and Borneo, all of which are supposed to be relics of an ancient southern continent, for whose existence prior to the Tertiary period there is much evidence. The Anura (frogs and toads) enjoy a much broader distribution than the tailed forms, being barred in their over-seas migration only from the most remote of oceanic islands. Their methods of dispersal will be discussed later (page 46).

For some reptiles, notably the Crocodilia and marine turtles, the seas of course afford no obstacle, the only practical limit to their distribution being that imposed by temperature. Among the most interesting of living reptiles are the giant tortoises, some of which have been in captivity for upwards of a hundred and fifty years. They are confined to-day entirely to certain oceanic islands—the Galapagos Islands off the coast of Ecuador (*galapago* being one of the Spanish terms for tortoise), and the islands of the western Indian Ocean, namely, the Mascarenes (Réunion, Mauritius, and Rodriguez), the Comoros, the Aldabras, the Amirantes, and the Seychelles. On the other hand, these tortoises are totally extinct on the mainland of South America, Africa, and Eurasia. Their shells are common as fossils, however, in India, Europe, and North America, in rocks of Miocene to Pleistocene age. As land tortoises are drowned within a few hours if they attempt to swim, their distribution could not have been accomplished by any overseas journey, but must indicate again former land connections over which they could travel.[1] Their present distribution is also within the limits of the ancient Gondwana land mentioned above.

[1] The geologic evidence seems to be partly at variance, in that the Galapagos are volcanic islands and may always have been such.

The serpents, many of which are fairly good swimmers, are incapable of passing large bodies of salt water of their own volition, with the exception of the specially adapted sea-snakes, which are found in the tropical seas, sometimes several hundreds of miles from land. Lizards in their adult condition are as incapable of passing an oceanic barrier as are the snakes, but, as Heilprin remarks, "it would appear that in some special way—whether as effected by the oceanic currents themselves or through the agency of birds—their eggs may be transported to very considerable distances out to sea, since this order of animals is sufficiently represented in remote islands where neither snakes nor amphibians have as yet been encountered."

With the birds, as we shall see, it is only the flightless forms, such as the ostrich, rhea, and cassowary, or the apteryx of New Zealand, which are debarred from trans-oceanic migrations, for even small birds are carried far on favoring gales.

With mammals, except those which, like the whales and seals, are especially adapted to marine life, bodies of water of a greater expanse than 20 to 50 miles are impassable when not frozen. Many mammals are, however, excellent swimmers, the jaguar being known to cross the broadest of the South American rivers, while the tiger and elephant, as well as the deer, will all take to the water freely; but it is doubtful whether any of them will venture out of sight of land. Heilprin summarizes as follows: although "it may safely be conceded, from our present knowledge on the subject, that while many of the land Mammalia can effect with safety, and even readiness, such water passages as are most generally to be met with on continental areas, none, probably, would be prompted to undertake a journey across an arm of the sea whose width measured 50 or more miles, or even one much exceeding half that extent. To these difficulties or impossibilities in the way of dispersion must be attributed the circumstance that the vast number of oceanic islands are deficient, except where man has effected an introduction, in representatives of this particular class of animals." The finding of allied or nearly identical forms of mammals upon land masses now isolated generally points to former land connections where none now exist.

Just as bodies of water prevent the passage of land animals, so *land masses* form barriers to the spread of sea life. Such, for instance, is Cape Cod, which separates the relatively cold waters of

Massachusetts Bay from the ocean to the south, with a very marked distinction in the contained faunas. The Isthmus of Panama is another case in point, while certain relic seas like the Caspian contain seals, porpoises, and other marine vertebrates whose forefathers entered it when it was an arm of the sea; their descendants being in turn cut off from the ocean with the severance of communication. A species of shark in Lake Nicaragua is another such zoölogical exile.

Impurity and Lack of Salinity of Sea-Water.—These afford an effective barrier to the dispersal of certain kinds of marine animals, such as the brachiopods, echinoids, crinoids, starfishes, squids, and foraminifers, but notably the corals and sponges. While there are fresh-water sponges, they form a very small proportion of the entire number which are extant, and none have skeletal structures. On the other hand, the corals are exclusively marine although a few are known in brackish and even in tolerably fresh water. These exceptions, however, are notable, for as a rule all such forms require a water of maximum purity and salinity. Hence it is that extensive coral reefs or sponge-growing areas are never found near the mouths of large rivers such as the Amazon, Orinoco, or Mississippi, each of which bears a great load of sediment seaward. The Great Barrier Reef of Australia extends along the eastern shore of that continent for a distance of 1500 miles, and along the entire adjacent coast the map fails to reveal a single river of importance, although there are a few relatively small streams.

Means of Dispersal

Animals and plants are so widespread over the surface of the globe that migratory routes must be many, despite the effective barriers which have been mentioned. The means of dispersal are:

Land Bridges.—Land bridges, such as those at Suez and Panama, both of which are of comparatively recent origin, geologically speaking, have nevertheless afforded the means whereby continents received their faunas. The Panamanian bridge is of particular interest because we know the history of its existence so well. There was evidently land connection between North and South America at least up to late Eocene time, although it has not always have been where the Isthmus of Panama now lies. While that connection existed there was free intermigration between the continents, but during a long period of severance—until Middle

Miocene time—no interchange of species was possible, and each fauna underwent a remarkable evolution, without the admixture of forms from the other. The re-formation of the land bridge, however, opened up the avenues of migration, and we find recorded the incursion of the more virile North American types into South America, such as the mastodons, horses, deer, wolves, and cats, and the immigration of South American forms, the ground-sloths, armadillos, and other species in exchange (see Chapter XXXVIII). Bering Strait, although now impassable except over the ice in winter, has been at various times in the geologic past a migratory route of the utmost significance, so important in fact that the land animals of North America and those of the Eurasian continent show the closest blood relationship, and this was especially true during Tertiary time. In fact, as Matthew says:

"The Alaskan bridge is in existence to-day, only a few yards of its planking removed, if one may so speak, the substructure intact, and the marks of the missing planks still showing on the undamaged portion." Actually the intervening water between America and Asia has a width of only 36 miles and a depth of from 23 to 30 fathoms, so that the comparatively slight elevation of 200 feet would afford dry and safe transit for the passing and repassing hosts.

Natural Rafts and Driftwood.—Terrestrial animals, either accidentally or with intent, occasionally take passage upon drifting material which enables them to accomplish over-water journeys which are sometimes of considerable extent. Many Arctic animals, such as the reindeer, will go out upon the ice to effect a crossing like that over Bering Strait, the Nova Zembla reindeer occasionally going to Spitzbergen, a distance of 240 miles; or such forms as the polar bear may venture out upon the shore ice for the seals or fish which constitute their prey. These bears are splendid swimmers, for one was observed by Captain Parry in Barrows Strait 20 miles from shore, with no ice in sight. Even such natatorial powers would not, however, take them to Iceland, and yet living bears are stranded on the Icelandic shores every year, no fewer than twelve having arrived in one season. In such instances, the journey was probably very largely accomplished by means of floating ice floes which had broken away from their moorings.

Natural rafts of vegetation are a very potent factor in dispersal.

These are masses of driftwood and leaves held together by a tangle of vines, creepers, and other vegetation, and sometimes having a covering of soil sufficient to maintain living plants or even trees. Such rafts are formed by the natural accumulations of timber along the rivers, caused by the caving of the banks on the outside of the river bends, and as larger masses are formed they are swept out to sea by the action of the stream. Such natural rafts have been reported several times more than a hundred miles beyond the mouths of some of the world's great rivers and in one recorded instance the distance traveled was over a thousand miles! Heilprin tells us that floating masses of wood, with upright trees growing over them, were mistaken by Admiral Smyth in the Philippine seas for true islands, until their motion made their real nature apparent. Such rafts often have quite an assemblage of animal life, such as monkeys, tiger-cats, squirrels, and arboreal mammals in general, together with reptiles and molluscs.

A boa, a huge species of snake, was transported 200 miles on a cedar tree to St. Vincent, and Heilprin records the landing of four pumas in a single night in the town of Montevideo. He goes on to say: "To what distance such a floating raft with its living cargo may ultimately be carried in safety, and without detriment to its inhabitants, over the oceanic surface there are as yet no data for determining. But there would appear to be no reason for assuming that they could not be transported to a distance of several hundreds of miles, seeing that the upright vegetation found on many of them would serve with powerful effect in the face of a wind. And while the majority of the animal inhabitants might be exterminated before the end of the voyage, the safe arrival on an island or distant shore of a very limited number of individuals, embracing both males and females, would serve in a short period, under favourable conditions, to stock the new land with the species. That an absolute limit is set, however, to migration as effected in this manner is proved conclusively by the utter absence in most of the oceanic islands of indigenous mammals, excepting bats."

Favoring Gales.—The forms aided by this means are the aërial nekton—insects, birds, and bats—and while all three can progress without the aid of favoring winds their flight is very largely increased thereby. This aid is perhaps largely accidental, nevertheless migratory birds are known to take deliberate advantage of it.

Insects present numerous instances of great powers of sustained flight when aided by air currents, of which the most conclusive are naturally those recorded at sea. The ship *Pleione*, on reaching a point some 960 miles south-west of the Cape Verde Islands, came upon hundreds of moths belonging to a species which is common in the Eastern Tropics, but is not found in South America, the nearest land. From the direction of the wind during the previous four days, it appeared to be beyond doubt that the insects had come from the Cape Verdes, and therefore must have crossed nearly a thousand miles of ocean! The nuptial flights of many insects often aid, either incidentally or designedly, in their dispersal, when taken upon windy days.

Bird flight is marvelous, and some recorded instances are credible only in these days of the perfection of the airplane. Many birds are known to pass several hundreds of miles on the wing without rest and it is highly probable that their unaided flight may extend over one or more thousand. The wild goose is supposed to fly at 60 to 75 miles an hour and the swallow at 90 or more, and many other birds may be nearly if not quite as speedy. A sustained flight of ten to twelve hours is not beyond belief, otherwise the enormous distances which certain migratory birds cover would not be possible. Land birds have been met with at all points in the transatlantic passage, but it is quite probable that passing craft afford temporary refuge to the weary ones. The prevailing westerly winds between 30° and 58° north latitude carry many birds all the way across, for the landing of American birds during or after heavy storms upon the coast of England and the island of Heligoland is no unusual thing. North of 58° the prevailing winds are easterly, so that the European birds are transported to America by way of Iceland and Greenland. The west to east passage is much easier, however, as the transatlantic airplane flights have repeatedly demonstrated. Bats are found the world over, even on the most remote sea isles, where they may be the only indigenous mammals. This is sufficient evidence for their migratory powers.

Migrations

Migrations are of two sorts: permanent or racial movements where there is some such impelling cause as the changing of climatic conditions, or the unendurable increase of competition for food, shelter, or safety at home. Many such are recorded and will

be recorded in human history, like the coming of the white men to America, while prehistory has innumerable instances of the same thing. A few such were the intermigrations between North and South America, already referred to; the world-wide dispersal of the elephants from their primal African home, and of the American camels into Asia, and their relatives, the llamas, into South America. For several such migrations of horse-like forms between North America and the Old World there is also abundant evidence.

Seasonal migrations also occur for food and for reproduction. Those for food occur in the temperate and frigid zones where the inclement weather of winter brings such scarcity of sustenance that animals must migrate or starve. The caribou of North America make such seasonal migrations and the American bison or "buffalo" were also known to do so. The migrations of many insects such as the "Rocky Mountain locust" are well known.

The most remarkable migrations are those for reproduction, for many animals have within them a wonderful homing instinct which impels them to seek out their own birthplace for the purpose of bringing forth their young. Under this head come the movements of certain fishes such as the herring and alewife into shoal waters along the coasts, and the shad, sturgeon, and salmon to the rivers. The last mentioned ascend the Columbia and Yukon for thousands of miles, passing all but impassable obstructions in their journey and wearing themselves out in its accomplishment.

Some bird migrants also cover thousands of miles, as, for example, a cuckoo which makes the annual journey from Fiji to New Zealand and return, an over-seas voyage of 1500 miles in either direction. The curlew-sandpiper breeds on the Siberian tundras, but goes in the northern winter to the Cape of Good Hope, Tasmania, and Patagonia down the three main continental axes (see map, Fig. 254). The Asiatic golden plover migrates from Alaska to Hawaii, a distance of 2000 miles, with no possibility of rest. Others, like the penguins, make their long migrations by swimming.

Of the mammals, the sea-lions or fur seals of Alaska excite our admiration, not so much from the length of their journey of 1500 miles but because of the apparent accuracy and precision of their navigation, always arriving at the beach in the Pribilof Islands, for instance, at approximately the same time and place as the year before; but, while their actual passage seems to be as mysterious

as that of a raiding submarine, it is largely controlled by seasonal changes in water temperature and the trend of ocean currents.

Zoögeographical Realms

Students of animal distribution have divided the world's surface into a number of distinct areas according to the likeness or unlikeness of their faunæ. These divisions are based very largely upon the distribution of mammals, but they serve nearly as well to show the dissemination of other terrestrial groups, though manifestly not at all for the birds or for marine types. Several plans have been proposed having many points of resemblance but differing in certain minor details. The boundaries and nomenclature given on the present map (Fig. 7) are largely those of W. L. and P. L. Sclater, proposed in 1899. The realms are plotted upon a polar projection map instead of the usual Mercator's projection, as the former renders the migratory routes much more intelligible.

Most naturalists agree in dividing the land surface of the globe into six primary areas, to which the term *realm* has been applied. These have been more or less divided into subrealms, some of which are in the nature of transition areas between the larger realms. The six realms are:

1. The ***Nearctic*** (Gr. νέος, new, and ἀρκτικός, arctic), embracing all of North America to the edge of the Mexican plateau and including all of the islands to the north, together with Greenland.

2. The ***Neotropical***, consisting of Central America south of the Mexican plateau, all of South America and the Antilles or West Indian islands.

3. The ***Palearctic*** (Gr. παλαιός, ancient), embracing the whole Eurasian continent, except that portion lying south of the northern line of Persia and Afghanistan, the Himalaya Mountains, and the Nan-ling Range in China, all of which are barriers of a physical nature which most animals cannot surmount. Africa north of the Sahara, Iceland, Spitzbergen, and the Arctic islands north of Siberia are included in this realm.

4. The ***Ethiopian***, including all of Africa and Arabia south of the Tropic of Cancer, although some authorities extend it north to the Atlas Mountains, making it thus include the entire Sahara. Madagascar and other small adjacent islands also come within this realm. It is almost exclusively tropical, more so than any other region.

FIG. 7. — Map of zoogeographical realms. Polar projection.

5. The ***Oriental***, consisting of the southern coast of Asia east of the Persian Gulf, the entire peninsula of India south of the Himalayas, India East, and the portion of China south of the Nan-ling Range (Malaysia). The islands of Sumatra, Borneo, Java, Celebes, and the Philippines are also included.

6. The ***Australian***, embracing Australia, New Guinea, Tasmania, New Zealand, and the oceanic islands of the Pacific.

Owing to the great similarity of their respective faunæ the Nearctic and Palearctic are sometimes grouped together as the Holarctic (Gr. ὅλος, entire) realm.

Lydekker has proposed three major terms to include the whole terrestrial surface, which made a strong appeal to the student of extinct as well as of living mammals, as they represent the three great areas of independent mammalian evolution (see continental adaptive radiation, Chapter XVIII). Lydekker would include Nearctic, Palearctic, Ethiopian, and Oriental regions, among which there has generally been more or less freedom of intermigration, in one great Arctogæic (Gr. ἄρκτος, north, and γαῖα, land) realm. South America or the Neotropical region was for a long time during the Tertiary isolated from the rest of the world and to it he has given the name Neogæa or the Neogæic realm. The third great realm, the Australian, which has been isolated since the beginning of the Tertiary, he calls Notogæa (Gr. νότος, south), and this is to-day the home of those living "Mesozoic" mammals, the marsupials, which competition has practically eliminated from the rest of the globe.

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CHAPTER IV

BATHYMETRIC DISTRIBUTION

Definition.—Bathymetric[1] distribution concerns itself with the vertical range of organisms in space, and means much more than mere altitude, for in passing from the highest alpine peak to the abysmal depths of the sea one would find a series of contrasting conditions which of necessity profoundly affect the organism. Of these the primary conditions are three. (1) The air or water medium, which determines the method of breathing, is, with few exceptions, in each case prohibitive to the inhabitants of the other. (2) The presence or absence of light not only modifies the animal directly but indirectly through its effect upon the food supply, for assimilative plants, which form the ultimate nourishment of all animate nature, cannot exist where light is wholly absent. (3) The third primary condition is the presence or absence of a substratum, without which the organisms must be self-supporting, either buoyant or able to swim. This condition therefore determines the bionomic group to which the animal belongs, whether plankton or nekton on the one hand, or benthos on the other (see Chapter II).

The secondary conditions limiting bathymetric distribution are whether the water be fresh or salt, and the increase of pressure with the depth—very slight for air-dwelling forms but relatively enormous for those dwelling in the sea.

Three Organic Realms

Hence from the bathymetric as well as from the geographic standpoint three organic realms may be recognized. The bathymetric divisions are:

1. *Geobiotic* (Gr. γῆ, land, and βιωτικός, pertaining to life) or terrestrial.

[1] Bathymetric (Gr. βάθος, depth or height, and μετρεῖν, to measure) is here used to cover the entire vertical range of organisms in accordance with the practice of Parker and Haswell and of Grabau. Other authorities limit it to the aquatic realm, using the term altitudinal for the distribution of terrestrial forms.

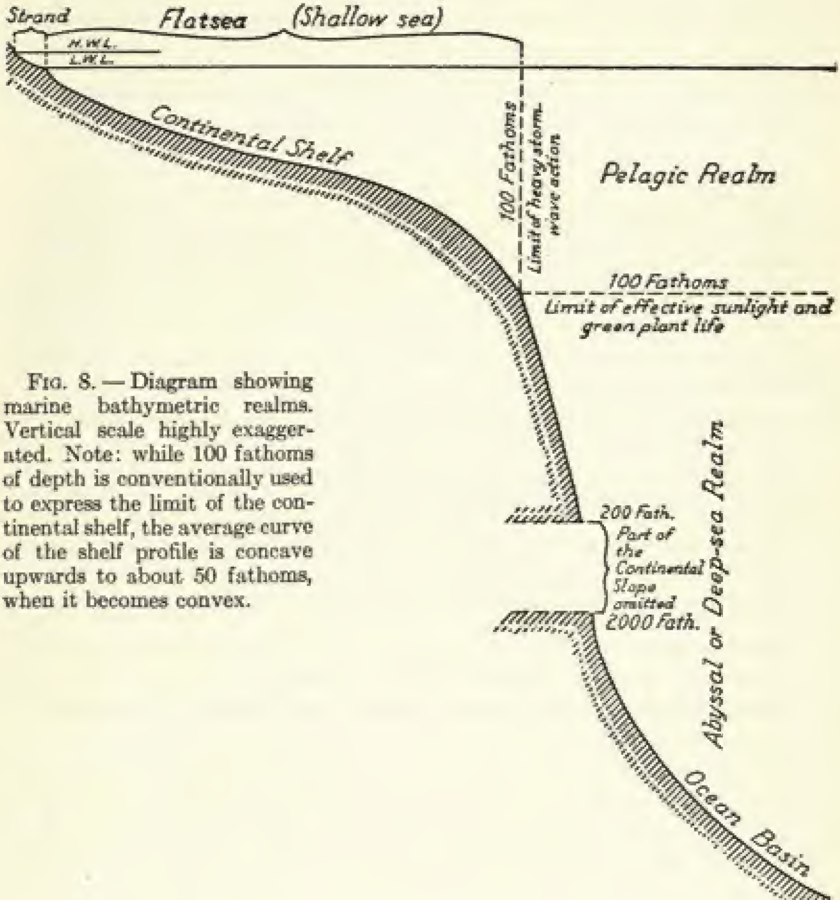

FIG. 8. — Diagram showing marine bathymetric realms. Vertical scale highly exaggerated. Note: while 100 fathoms of depth is conventionally used to express the limit of the continental shelf, the average curve of the shelf profile is concave upwards to about 50 fathoms, when it becomes convex.

2. *Limnobiotic* (Gr. λίμνη, lake) or fresh-water inhabiting (lakes or rivers).

3. *Halobiotic* (Gr. ἅλs, sea) or marine or salt-water inhabiting (the sea).

These three realms stand in marked contrast to one another, although, as we shall see, the inhabitants do intermingle to a certain extent at their lines of contact, which also give opportunity for permanent intermigrations.

Geobiotic or Terrestrial Realm

The terrestrial realm extends from high-tide mark along the shores of all continents and islands to the summit of the highest elevation. It ranges in altitude, therefore, from lowlands to the Alpine subregion, and each division—lowland, upland, prairie, high plain, or mountain range—has its own distinctive fauna and flora, governed by many influences, but in part at least by altitude. This last limits quite effectively the character of the flora, as for example the contrasting vegetation of the tropical Mexican coastal lowlands on the one hand and of the temperate high plateau on the other. The so-called timber-line, the limit of tree growth, is also governed by altitude, although varying in different regions, due to latitude and climate.

One additional terrestrial subrealm is the Cryptozoic (Gr. *κρυπτός*, to hide, and *ζωή*, life) or the subterranean caves, the only place in the geobiotic realm where light is absent. As we shall see in a later chapter (Chapter XXIII) this forms a limited biotic environment which profoundly affects its denizens. Internal parasites and the wood-boring larvæ of insects also dwell in a lightless environment and are consequently modified.

Limnobiotic Realm

The terrestrial waters contain a rather limited fauna, as comparatively few invertebrates have ever attained a foothold therein. This possibly is due in part to the freshness of the water, but also to the flowing character of the terrestrial waters, a condition to which the great majority of invertebrates with their mero-planktonic larvæ cannot adapt themselves. Certain lakes and relic seas are the only bodies of fresh water of sufficient depth to have the deep-sea characteristics of absence of light and increase of pressure, but we do not find such profound modifications in lacustrine forms as in those which people the abyss. This is probably due in large measure to the evanescent character of all lakes from the geologic point of view. They are individually so short-lived that there has not been time for any very marked adaptive characteristics to develop in their inhabitants. Thus, for instance, while luminescent or light-producing organs are so characteristic of deep-sea and nocturnal marine animals, none are found either in the deep lakes or in the equally evanescent caves, al-

though in each instance they might be very useful in the struggle for existence.

Halobiotic or Marine Realm

Biologically speaking, the most important bathymetric realm is the marine, for here we find all the contrasting characteristics abundantly developed, except, of course, the atmospheric medium, and in addition the ages during which the ocean has existed have afforded sufficient time for evolution to run its course.

The marine realm is divided into four subrealms, whose characteristics are as follows:

Strand,	light,	substratum	present	Littoral
Flatsea or shallow sea,	"	"	"	
Pelagic,	"	"	absent	
Abyssal,	dark,	"	present or absent	

Strand.—The strand or tidal zone is the transitional area between the marine and terrestrial realms, for here the inhabitants are left bare twice daily by the receding tide and have to endure drying, either by means of closable shells or other devices, or burrow down into the moist sands, or must be able to breathe both the air and the water. The tidal zone is of course of very variable extent, owing to the differing height of tides and the declivity of the strand itself, and ranges from a width of a few feet to several and in rare cases to many miles; in the Bay of Fundy, the tides, running into a constantly narrowing area, grow proportionately higher until they attain the greatest altitude recorded in the world, about 50 feet at the time of the highest tides. Thus in Minas Basin, full-rigged deep-water ships were seen lying in the red mud with no water in sight, and yet a few hours later they were borne on the bosom of the incoming tide.

Flatsea.—The term flatsea or shallow sea is applied to the waters overlying the continental shelf below low-water mark. This continental shelf is formed by the action of storm waves, which are continually cutting back the shore-line and depositing the débris, together with other land waste, upon the area, especially at its outer edge. This margin, which marks the extreme limit of wave action, is in round numbers about 600 feet below the surface of the sea, or at the 100-fathom line.

The continental shelf varies in extent, as does the strand, in-

creasing in width at both the inner and outer margins, and is narrowest along the newer shores of continents and islands and widest where the coastal area is old or possibly subsiding. The slope of the continental shelf is, in general, long and smooth, the bottom near the outer edge descending more or less rapidly to the more profound depths of the sea (see diagram, Fig. 8).

The flatsea is of the utmost importance biologically, for it has both light with its attendant vegetation, and a substratum whereupon benthonic organisms may dwell. Furthermore, its relative shallowness makes the presence of comparatively low physical barriers effective for the isolation which is so essential in evolution. All of these factors, light, plant-food, movements of the waters, warmth, and isolation, make the flatsea a veritable hot-bed of evolution. Its importance as such has been abundantly recognized, so that it has been called the "cradle of evolution."

"The shore-fauna is certainly the most representative of all faunas. What pictures rise in the mind! Swiftly moving infusorians lashing their way through the water; Foraminifera with beautiful shells of lime slowly gliding on the fronds of sea-weed; calcareous sponges like little vases and more irregular flinty- and horny-sponges, sometimes coating the rocks like the common crumb-of-bread sponge, sometimes growing in beds like the plants they were once supposed to be; hydroid zoöphytes like miniature trees on rock or sea-weed; sea-anemones and corals often like beds of flowers, living an easy-going life, waiting for food to drop into their mouths, or stinging small passers-by; unsegmented worms such as the 'living films' which glide on the sea-weeds or stones like mysteriously moving leaves, and the nemertines or ribbon-worms, also covered with cilia, but provided with a remarkable protrusible proboscis, sometimes ejected so violently as a weapon that it breaks off altogether and wriggles like a worm itself; the higher ringed worms or annelids in extraordinary numbers, like *Nereis*, *Phyllodoce*, and *Aphrodite* itself, so beautiful in themselves and in their names that we can understand the enthusiasm of the expert who is said to have named his seven daughters after seven favorite Polychæts; the starfish creeping up the rocks with their strange hydraulic locomotor system, the brittle-stars using their lithe arms like gymnasts, the sea-urchins tumbling along on the tips of their teeth, and the sluggish sea-cucumbers plunging their tentacles into the mud and then into their mouths; the beautiful colonies of 'moss-animals' or Bryozoa, crusting stone and weed as if with lace, or forming leaf-like fronds like the seamat (*Flustra*), which was one of the first animals Charles Darwin worked at, or growing into calcareous tufts as if in mimicry of corals; myriads of crustaceans, such as water-fleas, acorn-shells, beach-fleas, sandhoppers, no-body crabs, sea-slaters, shrimps, hermit-crabs, and shore-crabs proper; strange sea-spiders, neither crustaceans nor spiders, like *Pycnogonum littorale*, clambering

among the sea-weeds and hydroids; . . . bivalves innumerable, such as cockles and mussels, oysters and razor-fish; herbivorous gasteropods like periwinkles, and voracious carnivores like the dog-whelks and buckies; sedentary limpets with a slight range of movement and a slight memory for locality, since beyond a narrow radius they fail to find their way home; an occasional cuttle-fish caught in a shore-pool and many more further out; a large representation of ascidians or sea-squirts, both simple and compound, which lie at the base of the vertebrate series; the lancelets (*Amphioxus*) buried all but their mouth in the fine sand; true shore-fishes like sand-eels and gunnels and shannies; an occasional reptile like the lizard *Amblyrhynchus* which swims out among the rocks, or a poisonous sea-snake, or a turtle coming ashore to lay her eggs; numerous shore-birds like oyster-catcher and rock pipit, gull and cormorant; and an occasional mammal like otter and seal—on the whole *a more representative fauna than in any other life-area.*"

Keen Struggle for Existence.—"It is evident that the shore-area must be characterized by a keen struggle for existence. In the open sea there is practically no limit to the floating room and swimming room, but the shore is narrow and crowded. In a rock pool there is often no vacant niche. There is competition even for *foothold.* It is important, for instance, that the limpet which makes little journeys in search of sea-weed to nibble should not go too far, else it will not find its way back, and will have lost the spot which its shell has grown to fit. It is curious, too, to see the American slipper-limpet—one growing on the top of another to the number of four or five—suggestive of the root-idea of a skyscraper" (Thomson).

The term littoral is variously used but may include both the strand and flatsea.

Pelagic Realm.—The pelagic realm embraces all of the superficial waters of the ocean down to the depth to which effective sunlight penetrates. It is characterized physically by the presence of light and the absence of a substratum. In the upper portion there is variable temperature and frequent and violent wave action, while in its lower strata the movement of the waters and the temperature are greatly reduced.

The distance to which sunlight penetrates varies, being manifestly greater in the tropics where the sun's rays may be perpendicular to the surface of the sea, and less toward either pole where the rays become more and more oblique. By exposing photographic plates at various depths it has been ascertained that light penetrates in the tropics to a depth of 3250 feet, though this is true only of the ultraviolet and blue rays. Red and green rays fail to penetrate to 1625 feet, but at 325 feet all of the rays of ordinary bright sunshine are present, though red light is the least strong.

Assimilating plant life, which forms the ultimate food supply of all animals, is dependent upon the presence of these red, orange,

and yellow rays, which virtually restricts it to the upper 500 feet of oceanic waters. The importance of this is such that the vertical limit of the pelagic zone may be placed at about 600 feet or 100 fathoms; hence it becomes a seaward extension of the flatsea.

Owing to the absence of a substratum, however, no benthonic forms can exist in the pelagic realm, but all must be either nektonic or planktonic. The pelagic realm constitutes therefore the high seas, and is not only the meeting place of the commerce of all nations but the great means of dispersal for countless forms of marine life, including the mero-planktonic larvæ of shallow- and deep-water benthos.

Abyssal Realm.—The abyssal realm is that portion beyond the limits of the continental shelf and beneath the pelagic, and includes all waters below a depth of 100 fathoms. This realm may be divided into the abysso-pelagic zone, wherein there is no substratum, and all organisms, like those of the pelagic, must swim or float; and the abysso-benthonic zone, in which a substratum is present.

The main characteristics of the abyssal realm are:

1. *Absence of light.* Light of course must exist in the upper transitional strata but it lacks the rays essential to assimilating plant life, hence none exists. The animals therefore are all either carnivorous or feed upon dead organic matter, some of which is of plant origin (oozes, see Chapter XXIII). Below the transitional realm the darkness, except for organic luminescence, is profound.

2. *Quiescence.* There is an utter absence of movement aside from the sluggish ocean currents of the greater depths, the progress of which is immeasurably slow.

3. *Cold.* Below a certain depth, the waters in all oceans the world over have become permanently chilled nearly to the freezing point of fresh water, and all diurnal and seasonal variations of temperature and those due to the climatic zones cease to exist.

The mean temperature of the Atlantic at the surface is 68° F., at 500 fathoms 37°, at 1000 fathoms 35.6.° The Mediterranean, on the other hand, is warmer, owing to the barrier at the Strait of Gibraltar, which prevents the circulation of the deeper and colder waters. At equivalent depths the Mediterranean temperatures are: surface, 75° F., 500 fathoms, 55° F., and 1000 fathoms, 55°.

4. *Pressure.* The pressure of the abyssal waters is enormous, increasing directly with the depth, the ratio of increase being about

one ton to the square inch of surface for every thousand fathoms of depth, as compared with the normal air pressure of approximately 15 pounds to the square inch at sea-level.

Thus the abyssal realm constitutes a simple biotic environment of vast extent but of comparatively uniform and changeless character and hence one not conducive to rapid evolutionary change. None of the deep-sea creatures is old geologically speaking, for while from 25 to 35 Paleozoic genera are known in the present *shallow* seas, none of the animals which people the *deep* sea is older than the Mesozoic. They seem to be all migrants from shallow water which have become adapted to the deep-sea conditions, but there is in no instance the evolution of a new race of animals exclusively restricted to the abyssal realm (see Chapter XXIII).

Intermigrations

Intermigrations between the various benthonic realms do occur where opportunity arises. They are, as in the geographic migrations, both permanent and temporary, the latter being divided in turn into seasonal migrations for breeding and occasional journeys for food or retreat.

Permanent migrations shoreward have not been many. Of the plants, there have been only the numerous fuci or sea-weeds which extend above the limits of the strand from just below high-water mark to the limits of salt spray. Thus while strictly terrestrial, they still feel the influence of their ancestral home. Beyond this point the migration apparently cannot extend.

Of the animals, certain molluscs are also shoreward migrants, but these are gastropods only, for they alone seem able to combine air-living with locomotion; the bivalves, for instance, surviving exposure to the air by keeping the shell tightly closed, which makes any activity manifestly impossible. Examples of shoreward migrating snails are *Littorina* of Brazil, which climbs the mangrove trees, and *Ampullaria*, the connecting link between land and water snails. Of the Crustacea, there are several species of land crabs, of which one, *Birgus*, an ordinary crab-like form, is found far from the shore and even climbs mountains and trees, but returns to the sea-shore every year to breed, the marine habitat of the young indicating to us the ancestral home of the species. Another land crab, *Cenobita diogenes*, is one of the hermit crabs which utilize the cast-off shell of some gastropod for the protection of their

otherwise defenseless body. A specimen from the Dry Tortugas group of the Florida Keys actually had a fossil shell (*Livona pica*) for its habitation. It is possible that the terrestrial isopods, wood-lice and pill-bugs, were also derived from a littoral stock. Probably, however, most of the transitions have taken place through accident in the relic seas or lakes.

The transition from aquatic to terrestrial life on the part of the vertebrates, although doubtless occurring long ago, even previous to Devonian time, was another instance of permanent landward migration, but whether from the marine littoral, the land-locked seas (relic seas freshened into relic lakes), or from the originally fresh or terrestrial waters is not quite clear. Evidence, however, seems to point to the last supposition. The annual return of most amphibia to the limnobiotic rather than the halobiotic realm for the purpose of bringing forth their young points to the former as the ancestral habitat of the race (see Chapter XXIX).

Temporary shoreward migrations are seen in several fishes, notably the common eel, which may travel from one pond to another through moist meadow grass. *Periophthalmus*, a curious fish found along the shores of tropical seas, inhabiting the mud-flats at the mouths of the various tropical rivers of the Old World, is popularly known as the walking fish or mud-skipper, as it emerges freely from the water for hours at a time, progressing by means of its curiously modified pectoral fins. The lung-fishes (Dipnoi), whose swim-bladder is modified to serve as a lung, can also live a long time out of water. While there is evidence that the Dipnoi are the survivors of a widespread group of fishes, they are all confined to the fresh waters of Australia, Africa, and South America to-day. The climbing perch, *Anabas*, which inhabits fresh waters and estuaries in Africa and the oriental region, not only comes ashore but actually climbs trees to the height of several feet by means of the strong spines on its pelvic fins and gill-covers (see Fig. 130).

Permanent Seaward Migrations.—Of plants there are eight species of sea-grasses which have become adapted to salt-water life. The mangrove trees make their homes along tropical shores within the reach of the tides, but while the roots and portions of the trunk may be entirely submerged, the crown of leaves is always in the air; the grasses of which mention has just been made may, however, be wholly below the surface of the water.

Of arthropods, there are a number which have become entirely marine, although of terrestrial origin, notably the sargassum insects which live among the floating fronds of the gulf weed and a spider (*Desis*) found in rocky crevices along the shore. Of the vertebrates, the marine migrants belong only to the three higher classes, land-to-sea migrations on the part of fishes being *a priori* impossible and on the part of amphibia rare, as salt water is distasteful if not actually fatal to them. Doctor Gadow says that common salt is poison to the amphibia, nevertheless we have reports of little frogs of the genus *Rana* hopping about on the flats of a tidal creek opening into Manila Bay, and two holes made by a crab were seen to be full of wriggling tadpoles newly hatched. The tadpoles were developing in only slightly diluted sea-water. However, even though occasional temporary migrations may occur, there is no instance at present or in the geologic past where amphibia have become permanently adapted to marine life.

Of marine reptiles, however, the tale is a very different one, for not only are there several different sorts—marine turtles, crocodiles, and sea-snakes—living to-day, but the geologic record is crowded with remains of sea-going Reptilia—plesiosaurs, the wonderfully adapted, dolphin-like ichthyosaurs, the Cretaceous sea-serpents or mosasaurs, and many others, all of which have become extinct.

Of birds, many, like the gulls, terns, frigate-bird, auks, and petrels, make their home on the bosom of the sea, but none perhaps is so thoroughly adapted as the great wandering albatross which follows a ship for miles without resting, and has almost entirely forsaken the land as an abiding place, except for breeding.

Among ancient forms, *Hesperornis* (see Pl. XV) from the marine Cretaceous strata of our great West was an admirable instance of a sea-adapted bird. It had lost completely all powers of flight, while the retention of reptile-like grasping teeth in its jaws and its inclusion in marine sediments in association with plesiosaurs, mosasaurs, and other marine reptiles and fishes give indubitable evidence of its habitat.

Of mammals, the seals, whales, and Sirenia or sea-cows are instances of permanent seaward migration, possibly by way of the terrestrial rivers or estuaries. The resultant modifications of these as well as of certain of the marine reptiles, which will be discussed

in Chapter XX, are so profound as to render their return to the ancestral habitat either a relatively rare temporary migration, as in the sea-turtles and seals, or an impossibility, as among the ichthyosaurs and whales.

Temporary Seaward Migrants.—Of temporary seaward migrants, the most noteworthy is the curious iguana-like lizard *Amblyrhynchus cristatus* (see Fig. 53) which is found in the Galapagos Islands. Darwin says of it: "It is extremely common on all the islands throughout the group, and lives exclusively on the rocky sea-beaches, being never found, at least I never saw one, even ten yards in-shore. . . . Their tails are flattened sideways, and all four feet partially webbed. They are occasionally seen some hundred yards from the shore, swimming about. . . . When in the water this lizard swims with perfect ease and quickness, by a serpentine movement of its body and flattened tail—the legs being motionless and closely collapsed on its sides. . . . I opened the stomachs of several, and found them largely distended with minced sea-weed (Ulvæ), which grows in thin foliaceous expansions of a bright green or a dull red colour. . . . I have reason to believe it grows at the bottom of the sea, at some little distance from the coast. If such be the case, the object of these animals occasionally going out to sea is explained. . . . The nature of this lizard's food, as well as the structure of its tail and feet, and the fact of its having been seen voluntarily swimming out at sea, absolutely prove its aquatic habits; yet there is in this respect one strange anomaly, namely, that when frightened it will not enter the water. Hence it is easy to drive these lizards down to any little point overhanging the sea, where they will sooner allow a person to catch hold of their tails than jump into the water. . . . Perhaps this singular piece of apparent stupidity may be accounted for by the circumstance, that this reptile has no enemy whatever on shore, whereas at sea it must often fall a prey to the numerous sharks. Hence, probably, urged by a fixed and hereditary instinct that the shore is its place of safety, whatever the emergency may be, it there takes refuge."

Among mammals, temporary seaward migrants include the polar bear but especially the sea-otter, the latter being of particular interest in illustrating the course of evolution which the seals must have undergone in their adaptation to permanent marine life. This otter (*Enhydris*) was still comparatively plentiful all

along the northern Pacific coast in the middle of the last century, but because of its valuable fur has been almost entirely extirpated. It is well adapted for aquatic life, with hind feet suited only for swimming, back teeth with smooth rounded crowns for crunching "shell-fish," and in the care which the mother shows for the pup,—dandling it and diving with it.

Another very remarkable seaward migrant is the hippopotamus, which while really a terrestrial or river-inhabiting form, occasionally takes to sea in its passage from one river-mouth to another along shores which would be otherwise difficult to traverse.

Permanent Migrations from Sea to Fluviatile Realm.—In all probability the molluscs (fresh-water clams, mussels, and snails), the crustaceans, and the crayfish represent permanent or land-locked migrants from salt to fresh waters; but the great host of marine invertebrates have never succeeded in gaining a permanent foothold in the fluviatile realm. There are some curious instances of creatures, vertebrates and invertebrates, however, which have made what might be called involuntary migrations into fresh water. Such animals are found in what are known as relic seas, formerly in direct open communication with the oceans but now cut off from them. The best-known examples of these are the Black Sea and the Caspian Sea, both of which once widely connected with the Mediterranean, but have been freshened gradually through the inflow of rivers. The animals which inhabit these seas are also relic faunas or relic species which upon being cut off from their ocean-living brethren have adapted themselves to the gradually freshening waters. In the Caspian Sea, for instance, while there are comparatively few different *kinds* of animals, the fishes are so abundant in *individuals* that the fisheries are equal to those of the northern Atlantic Ocean. The fauna includes sturgeon, salmon, herring, porpoises, and seals. American examples of relic seas are possibly Lake Ontario but more especially Lake Champlain. The elevated beach deposits of Lake Champlain contain an abundance of marine shells and the bones of seals and whales.

Temporary Migrations from Sea to Fluviatile Realm.—There are a number of fishes, such as the shad, alewife, sturgeon, and salmon, which, while the major portion of their life is spent in the sea, ascend rivers periodically to spawn. Of these the most nota-

ble are the salmon, which ascend the Sacramento River to its extreme source, a distance of about 400 miles. In the Columbia they ascend as far as the Bitter Root and Sawtooth mountains of Idaho, a distance of nearly a thousand miles; but their extreme limit is not known. In the Yukon a few ascend to Caribou Crossing and Lake Bennett, 2250 miles. "At these great distances, when the fish have reached the spawning grounds, besides the usual changes of the breeding season, their bodies are covered with bruises, on which patches of white fungus (*Saprolegnia*) develop. The fins become mutilated, their eyes are often injured or destroyed, parasitic worms gather in their gills, they become extremely emaciated . . . and as soon as the spawning act is accomplished, and sometimes before, *all* of them die. The ascent of the Cascades and the Dalles of the Columbia causes the injury or death of a great many salmon" (Jordan). This wonderful instinct again points to the salmon and other fishes having originally been fresh-water forms which have made a permanent migration seaward in some bygone period, but the homing instinct still impels them to return to their ancestral waters to bring forth their young, even though the act be suicidal so far as the individual is concerned.

Permanent Migrations from Fluviatile Realm to Sea.—If, as certain authorities claim, the land waters are the ancestral home of all vertebrates (see Chapter XXVIII), the marine fishes must have all come from one or more ancient seaward migrants from the fluviatile realm. It has also been argued that the Cetacea, some of which, like the blind fresh-water dolphins (Platanistidæ), inhabit the rivers of India, made the limnobiotic realm their transitional habitat in their ancestral migration from land to sea. This, however, has not been proved, although the supposition that they were at least estuary-inhabiting forms before taking to the high seas is certainly plausible.

Temporary Migrations from Fluviatile Realm to Sea.—Of transitory migrants perhaps the most notable is the ordinary fresh-water eel. The eels of Europe spawn in a restricted area of the western Atlantic, in the vicinity of the West Indies, and the feeding grounds of the American forms are in the same vicinity. Thomson thus describes their life history: "The early chapters of the life-history remain obscure, but the young larva rises to the upper sunlit waters as a transparent, sideways-flattened, knife-blade-like creature, about three inches in length, with no spot of

color save in its eyes. It lives for many months in this state—known as a Leptocephalus—expending energy in gentle swimming, but taking no food. It subsists on itself, and becomes shorter and lighter, and cylindrical instead of blade-like. It is transformed into a glass-eel, about two and a half inches long, like a knitting needle in girth. It begins to move toward the distant shores and rivers. In some cases it may take more than a year to reach the feeding ground—those that ascend the rivers of the eastern Baltic having journeyed over three thousand miles. Their ranks are thinned, but large numbers succeed in finding the estuaries, and the passage of millions of elvers up our rivers is one of the most remarkable sights of Spring. There is a long period of feeding and growing in the slow-flowing reaches of the rivers and in the fish-stocked ponds. But there is never any breeding in fresh water, and after some years a restlessness seizes the adults as it seized the larvæ—a restlessness due, however, to a reproductive, not to a nutritive motive or impulse. There is an excited return journey to the sea—they don wedding garments of silver as they go and become large of eye. They appear to migrate hundreds of miles, often at least out into the Atlantic to the verge of the deep sea, where, as far as we know, the individual life ends in giving rise to new lives. In no case is there any return." This is an instance of former salt-water fish which having made a permanent migration into the fresh waters in some remote time, still seek not only their own birthplace but that of the race for the purpose of bringing forth their own young.

Migrations from Sea to Air and Air to Sea.—The intermigrations between the sea and the air are relatively few. Under migrations from sea to air would come as temporary intermigrants the flying fishes, of which several genera, representing a number of separate evolutions, are known. Their aërial existence is very transitory, as the flights, if such they are, rarely exceed a hundred yards and are generally far shorter.

Of air to sea migrants the penguins are perhaps the best example, they as have lost entirely the power of aërial progression, but their wings, through the degeneracy of the feathers and a compensating broadening of the entire structure, have become admirable swimming devices for what may be called submarine flight.

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CHAPTER V

GEOLOGIC DISTRIBUTION

The distribution of animals and plants in *time* is fully as important to our understanding of evolution as their distribution in *space*, for while the biologist who bases his research upon recent forms alone need concern himself with the latter distribution only, the student of the documentary evidences of evolution, which are, after all, the final court of appeal, is concerned very deeply with the former. The reader is referred to an Historical Geology such as Schuchert and Dunbar's for a complete understanding of the basis for the divisions of geologic time, but the following statements will suffice for our purpose.

The science of geologic chronology is the result of nearly two centuries of growth, and while the major divisions of earth's history and their limitations are now pretty well understood and agreed upon, there are yet many details to be adjusted. "Geology," says Schuchert, "was at first a science of minerals and rocks, and it was not until the significance of fossils as determinants of age was first worked out in England by Smith (1799–1801) and still more clearly by Cuvier and Brongniart in France (1808–1811), that stratigraphy and geologic chronology had their beginning." Then arose the doctrine of Catastrophism, advocated by Cuvier and D'Orbigny, a doctrine by which geologists, with the exception of Lyell, were largely swayed until the appearance of *The Origin of Species*, when they gradually came to a belief in the continual evolution of life. The idea of Catastrophism has now given way to the theory that it is environmental changes, local or general, that bring about changes in organisms. Hence the basis for the geologic sequence is the fossils that were buried in the rocks at the time the latter were formed. In the long earlier portion of the earth's history, however, the life was very rarely preserved, and the age of the rocks has to be determined by other methods.

Eras.—Geologists, as a result of study of the rocks with their contained evidences of changing environmental conditions, have divided the earth's past history into a number of major divisions

GEOLOGIC CHRONOLOGY FOR NORTH AMERICA

Eras	Major Divisions	Periods and Epochs	Advances in Life	Dominant Life
PSYCHOZOIC		Recent (Post-Glacial)	Rise of world civilization The era of mental life	**AGE OF MAN**
		Cascadian Revolution		
CENOZOIC (MODERN LIFE) 4%	QUATERNARY	Pleistocene	Periodic glaciation Extinction of great mammals	**AGE OF MAMMALS AND MODERN FLORAS**
	TERTIARY	Pliocene	Origin of Man	
		Miocene	Culmination of mammals	
		Oligocene	Rise of higher mammals	
		Eocene	Vanishing of archaic mammals	
		Paleocene	Rise of archaic mammals	
		Laramide Revolution		
MESOZOIC (MEDIEVAL LIFE) 11%	LATE MESOZOIC	Cretaceous	Extinction of great reptiles	**AGE OF REPTILES**
			Extreme specialization of reptiles	
			Rise of flowering plants	
	EARLY MESOZOIC	Jurassic	Rise of birds and flying reptiles	
		Triassic	Rise of dinosaurs	

GEOLOGIC CHRONOLOGY FOR NORTH AMERICA (*Continued*)

<table>
<tr><th>Eras</th><th>Major Divisions</th><th colspan="2">Periods</th><th>Advances in Life</th><th>Dominant Life</th></tr>
<tr><td></td><td></td><td colspan="3">Appalachian Revolution</td><td rowspan="5">AGE OF AMPHIBIANS AND LYCOPODS</td></tr>
<tr><td rowspan="8">PALEOZOIC (ANCIENT LIFE) 30%</td><td rowspan="4">LATE PALEOZOIC OR CARBONIFEROUS</td><td colspan="2" rowspan="2">Permian</td><td>Extinction of ancient life</td></tr>
<tr><td>Rise of land vertebrates
Rise of modern insects and ammonites
Periodic glaciation</td></tr>
<tr><td rowspan="2">Carboniferous</td><td>Pennsylvanian</td><td>Rise of primitive reptiles and insects</td></tr>
<tr><td>Mississippian</td><td>Rise of ancient sharks
Rise of echinoderms</td></tr>
<tr><td>MIDDLE PALEOZOIC</td><td colspan="2">Devonian</td><td>Rise of amphibians
First known land floras</td><td rowspan="2">AGE OF FISHES</td></tr>
<tr><td rowspan="3">EARLY PALEOZOIC</td><td colspan="2">Silurian</td><td>Rise of lung-fishes and scorpions</td></tr>
<tr><td colspan="2">Ordovician</td><td>Rise of land plants and corals
Rise of armored fishes
Rise of nautilids</td><td rowspan="2">AGE OF HIGHER (SHELLED) INVERTEBRATES</td></tr>
<tr><td colspan="2">Cambrian</td><td>Rise of shelled animals
Dominance of trilobites
First known marine faunas</td></tr>
<tr><td></td><td></td><td colspan="3">Grand Canyon Revolution</td><td></td></tr>
<tr><td>PROTEROZOIC AND ARCHEOZOIC 55%</td><td></td><td colspan="3">Evidences of life very scanty.
Protozoa. Protophyta.</td><td></td></tr>
</table>

called eras, the names of which indicate the degree of evolutionary advancement of life; thus, beginning with the most ancient, Archeozoic (primal life), Proterozoic (primitive life), Paleozoic (ancient life), Mesozoic (medieval life), Cenozoic (modern life), and Psychozoic (mental life).

Periods.—The eras in their turn are divided into periods, the names of which are in large measure geographic; that is, they were taken from the locality where the rocks pertaining to the period were first described, or they may be of historic significance in the development of the science. Thus, the names Cambrian, Ordovician, Silurian, and Devonian take their origin from the ancient inhabitants of England or Wales, or from the districts where the rocks are best developed; Triassic refers to the tripartite division of the rocks of that period in Germany; Jurassic to the Jura Mountains in Switzerland, in which the strata are admirably displayed; while Cretaceous, a relic of the old days of mineral geology, is from the extensive chalk deposits pertaining to the formation in Western Europe.

Epochs.—Subdivisions of periods have been called epochs. The epoch terms of the Cenozoic and Psychozoic eras are Eocene (dawn of the new), Oligocene (few of the new), Miocene (a minority of the new), Pliocene (a majority of the new), and Pleistocene (most of the new). Popular names, such as "Age of Man" for the Psychozoic era or "Age of Mammals" for the Cenozoic, are also in general use.

Reduced to its last analysis, the limits of all these eras, periods, and so on are due to certain more or less profound changes, climatic and otherwise, which have as one basic cause the warping of the earth's crust due perhaps to shrinkage of the earth's mass, giving rise not only to land elevation and often extensive mountain making, but to the alteration of the strand-line or line of demarcation between land and sea. This implies of course inroads of the sea upon the land, with the severance of old migratory routes and the restriction of terrestrial habitats, or the withdrawal of the waters and the formation of new land-bridges or the resurrection of those which formerly existed but which have been temporarily destroyed. It will be readily seen how profound an influence upon the evolution of life such movements may have—and there were many of them—especially when we bear in mind the attendant climatic changes, some of which were of a very marked character

(see Epilogue). For changes of climate react directly upon plant life and hence both directly and indirectly upon that of animals, while restriction or amplification of habitat and the severance or formation of land-bridges provide the essential isolation, or by the introduction of new forms increase competition, both of which stimulate evolutionary progress. Hence it is that evolution is not a uniform process, but where profound geologic changes are recorded, the tide of life flows more swiftly, and on the other hand, during the long periods of comparative quiet, evolution is slowed down to an almost imperceptible rate of change. The times of rapid progress Cope called "expression points" in evolution, and the rhythm is more or less synchronous with the physical changes which time has wrought in the earth itself.

Geologic Time Scale.—A convenient time scale has been worked out, knowledge of which is fully as important to a student of evolution as is a general idea of the geographic or bathymetric divisions of the earth's surface. It follows in general the geologic time-tables of Schuchert and Barrell. (See pp. 68 and 69.)

Age of the Earth.—An estimate of the earth's age in terms of years has been for a long time a subject of discussion, but the results vary astonishingly, as the following statement compiled from Schuchert will show.

The data are from two sources, Geology and Physics. The former science utilizes two chief methods; the rate of sedimentation and denudation and that of the accumulation of salt in the oceans derived from the weathering of igneous rocks and brought to the sea by rivers.

The known sedimentary rocks, if taken together, form a mass at least 70 miles thick, and this represents the algebraic sum of what was deposited and what has been irrevocably lost through denudation, so that the actual amount deposited must greatly have exceeded this total. What remains, however, represents "the wearing away to sea level, one after another, of more than 20 ranges of mountains like the present European Alps or the American Rockies." In addition there were long periods when the lands were so near base level that both erosion and the accumulation of sediments practically ceased. Upon such data as these, the rate of denudation and accumulation being estimated from modern evidences, figures are arrived at which are appallingly great. Thus Barrell gives minimum and maximum time values.

as follows, the figures representing millions of years: Cenozoic 55 and 65, Mesozoic 135 and 180, Paleozoic 360 and 460, and the sum from the beginning of the Paleozoic 550 to 700. The saline records are materially less; the leading geologists, however, accept estimates of from 250,000,000 to 300,000,000 based upon the above data, with perhaps 500,000,000 since the beginning of the Archeozoic.

The calculations of the physicists were likewise from two sources, the radiation of heat from the earth, based upon the assumption that it was once a molten mass and has cooled to its present condition, an idea which is not now generally accepted, and the time necessary for the reduction of certain radioactive substances, such as uranium and thorium, to stable lead. The radioactive calculation gives figures varying from 130 millions to one and one-half billions of years!

Estimates of geologic time are thus summarized by Schuchert and Dunbar: "It appears probable that the beginning of the Cenozoic was about 60,000,000 years ago, of the Mesozoic about 200,000,000 years, and of the Paleozoic about 500,000,000 years. Since the oldest dated rocks are intrusive into still older schists, it is probable that the earth is at least 2,000,000,000 years old."

Records of Life.—The records of past life are the fossils entombed in the rocks. These are the actual relics of animals and plants which lived in past geologic ages, and their nature and the methods of their preservation and their interpretation will be discussed more fully in Chapter XXV. They are found only in sedimentary as opposed to igneous or volcanic rocks, that is, in limestone, sandstone, or shales. Of these the majority were formerly water-borne aqueous sediments, such as sands or muds, while those composed of fine sand or dust carried by the winds (æolian) are comparatively rare. Of the aqueous rocks the marine, especially those formed in relatively shallow waters bordering upon the continents, are the most extensive, hence the record of marine life is far more complete than that of any other realm. Fresh-water deposits make up for their rarity by their importance, for they contain practically all of the relics of terrestrial life. This last record is very much broken, due either to a lack of deposition or to subsequent erosion.

Climatic Variations.—At the present day, the earth presents a variety of climatic conditions, ranging from the equatorial belt or

torrid zone where heat predominates, through the temperate zone where the climate is milder but where extremes both of heat and cold sometimes prevail, to the polar regions where intense cold is the rule. Not long ago, however, geologically speaking, the temperature throughout the world was much colder than now, though there were long intervals during the Glacial Period of almost uniformly mild conditions. The warm climates persisted during long geological ages, and even though there were zonal belts and fluctuations in the temperature, the polar areas contained warm-climate animals and plants. The temperature fluctuations were greatest toward the beginning and end of periods and there is also evidence of increasing aridity at such times.

Between the long warm times are short cool to cold periods. Seven periods of such temperature reduction are now known—earliest and latest Late Proterozoic, Silurian, Permian, Triassic, Cretaceous-Eocene, and Pleistocene. Four of these were glacial in nature. Curiously, these reduced temperatures were not geographically constant in their appearance, those of the earliest Late Proterozoic and the Pleistocene affecting the northern hemisphere, whereas in latest Proterozoic and Permian times the cooled area lay rather in equatorial regions. These cooled climates seem to appear as a rule toward the close of periods or eras, when the lands are greatest in extent and highest above sea level; and the glacial ones apparently accompany or directly follow the revolutions, when the earth's surface is being pushed up into mountains. (Schuchert.)

Summary of Geologic History

As human history is divided into ancient, medieval, and modern periods, so geologic history is comparably divisible into eras, the Paleozoic, Mesozoic, and Cenozoic. Human existence, however, far antedates written history, there having been what historians are wont to call the legendary period, now pretty generally known as the prehistoric. In a like manner there stretches back from the beginning of the fossil records of the Paleozoic a time inconceivably vast, during which life must have existed upon earth, but the evidence for its existence is either meager or argumentative, reasoned from the perfection which it had attained when legible fossil remains first appear, and which implies a long antecedent evolution; or based upon the large deposits of limestones, graphites,

and iron-ores which, so far as our knowledge goes, are mainly of organic origin.

Pre-Cambrian

Archeozoic and Proterozoic.—The great legendary eras are the Archeozoic and Proterozoic, the former of which is called the Age of Unicellular Life, for undoubted fossils of this time are as yet almost utterly unknown and it has been inferred that the dominant forms of plant and animal life were all unicellular forms, Protophyta and Protozoa, of very lowly organization.

In the Proterozoic, while known marine fossils are extremely rare and imperfect and almost indecipherable, they nevertheless indicate a very material evolutionary advance. The evidence is positive for the existence of marine algæ among plants, some radiolarians, sponges, and tubes and burrows made by annelid worms. But because of their position in the scale of animal life, the tubes and burrows imply Annelida and these in turn the more lowly organized sponges, cœlenterates, and other worms. This Proterozoic era, especially its latter half, may therefore be called the Age of Primitive Marine Invertebrates.

Paleozoic

Cambrian.—By Lower Cambrian time all the main invertebrate phyla had been evolved and possibly the vertebrates, as the fishes were well established by the Middle Ordovician. The degree of perfection of the invertebrates at the beginning of Paleozoic time shows that more fundamental evolution had taken place up to this time than subsequently. The main evolutionary structure of all invertebrate types having been established, their future changes are mainly concerned with detail and with the rise of certain important groups, such as the insects.

Ordovician.—The Ordovician saw the rise of the progressive cephalopods and the first recorded fishes, with whose development the trilobites, the highest and most aggressive form of Cambrian life, began to wane, ultimately to pass out of existence with the close of the Paleozoic. The active and carnivorous cephalopods became more and more important during the Ordovician and Silurian, to be gradually displaced by the fishes; the cephalopods persisted, however, in considerable numbers until the close of the Mesozoic, when they were reduced to the comparatively unimportant place which they now hold. By far the vast majority of

Paleozoic invertebrates were sedentary benthonic forms, feeding upon microörganisms or organic débris, though some were vagrant, living upon the benthonic sea-weeds, and others, like the starfishes, were carnivorous. The Ordovician rocks give us the first meager evidence of land plants, for while none are known prior to that period, the woody kinds appear before its close. To the Ordovician period, therefore, we owe the origin of two most important groups of organisms, the woody plants and the fishes among the vertebrates.

Silurian and Devonian.—The Silurian and Devonian periods collectively constitute the Middle Paleozoic, in contrast to the Early Paleozoic of which we have been speaking. They also usher in two events of prime importance to the animate world, the development of air-breathing forms on the part of both invertebrates (Silurian) and vertebrates (Devonian). In rocks of Silurian age we have recorded the first scorpion as well as fishes whose organization is in many respects similar to that of the double-breathing lung-fishes of to-day. Out of this ancient lineage, although we have not yet recognized their undoubted ancestors, were to come the Amphibia, which in turn gave rise to all the later terrestrial vertebrates. From the Devonian rocks we have not only the earliest footprint of an amphibian (*Thinopus antiquus*, Fig. 135) but also the actual skeletons. The latter have been found in Greenland in 1938. Fishes developed so wonderfully that the name Age of Fishes has often been applied to the Devonian period.

Terrestrially the late Silurian and early Devonian were characterized by increasing aridity of climate, which seems to have been the impelling cause in the evolution of air-breathing vertebrates through the drying up of the streams and lakes wherein their forebears among the fishes made their homes (see Chapter XXIX). The Devonian was also the time of the establishment of the first land flora.

Mississippian, Pennsylvanian, Permian.—The Carboniferous, which is now divided into the Mississippian and Pennsylvanian periods, together with the Permian, constitutes the Late Paleozoic, a time characterized in its earlier part by a mild, moist climate which, however, grew more and more severe toward the close and culminated in the middle Permian ice age. The Carboniferous was therefore the great age of coal plants, the vegetation reaching its

maximum development in variety and in the size of the individual plants during the Pennsylvanian period. Our knowledge of the plants of the time, however, is restricted to those of the low-lying swamps and we know nothing whatever of the upland flora. The coal plants were principally spore-bearing, of rapid growth, and soft, spongy woods. Seed-bearing trees and shrubs of many kinds were also present but their flowers were small and inconspicuous. Owing to their great carrying power the spores were very widely disseminated, giving the forests a very uniform character the world over.

During the Mississippian, sharks were the dominant fishes in the seas and oceans. They were of many kinds but consisted principally of the more ancient shell-feeding types which were subsequently almost wholly blotted out. The Pennsylvanian with its widespread coal swamps formed an admirable habitat for the development of land animals, spiders, scorpions, centipedes, ancient insects, and snails among the invertebrates, and amphibians among the vertebrates. Probably before the close of this period true reptiles, such as had abandoned the ancestral gill-breathing even in the adolescent condition, appeared. Of this there is direct evidence, and in addition the deployment of reptiles in the Permian implies their existence during the preceding period.

In Permian time the flora underwent a change; harsher conditions, following the warm moist climate of the Pennsylvanian, either destroyed the old cosmopolitan plant life or impelled its evolution into hardier sorts of vegetation. A new flora then arose, especially in the southern hemisphere where the change began, because the ice age was here most dominant in middle Permian time and spread thence throughout the world. This flora, consisting mainly of modern ferns, conifers, ginkgoes, and cycads, became the dominant vegetation throughout the Mesozoic until supplanted by the modern flora in Cretaceous time. Due to the stress of climate the insects developed those wonderful larval adaptations, seen in the metamorphosis of living insects, that enable them to live through the winter in the resting or pupal condition (see Chapter XXVII).

The passing of the Paleozoic, which was marked by the culmination of the Appalachian Revolution, also saw the extinction of many forms of ancient life, especially among plants and invertebrates. Of the latter, those which survived have altered little in

the ages which have since elapsed, while the vertebrates, especially the reptiles, birds, and mammals, have undergone practically their entire evolution.

Mesozoic

Triassic and Jurassic.—The Mesozoic era or Age of Reptiles is justly so called, for although all five classes of vertebrates (fishes, amphibians, reptiles, birds, mammals) were probably present throughout its entire length, the reptiles were the dominant forms of life. During the Triassic there were many kinds, some partially or wholly aquatic, others terrestrial. The Jurassic saw great numbers of reptiles inhabiting the land, the air, and the sea, and toward its close an immensity of size on the part of some of them which has never been equalled before or since among either terrestrial or semi-aquatic forms. The Jurassic also records the first flying reptiles and reptile-like birds, although the degree of their development again implies their existence during the Trias.

Cretaceous.—The Lower Cretaceous witnessed the rise of flowering plants and the extinction of the reptiles of huge bulk, such mighty forms being as a race usually short-lived, geologically speaking. The Upper Cretaceous saw the modernizing of the flora so that the forest plants would now wear a familiar aspect, although in unfamiliar combinations. The land reptiles soon reached the height of their specialization and while not as huge as those which had gone before, exceeded them in grotesqueness and bizarre appearance. Toward the close of the Cretaceous more conservative forms again prevailed. Mammals were numerous though still small and unspecialized, while the birds were essentially modern except that in all known examples they still retained the teeth characteristic of their reptilian ancestors.

With the close of the Mesozoic, which was marked again by great crustal changes, the so-called Laramide Revolution, came the extinction of the dominant reptilian types on land and sea, thus preparing the way for the evolution of the warm-blooded mammals, which were to be the ruling dynasty of the Cenozoic as the reptiles had been the overlords of creation during Mesozoic times.

Cenozoic

During the Cenozoic era or the Age of Mammals, the vegetation was of modern cast and life conditions in the main were similar to those of to-day, although there is much evidence of a gradual

elevation of nearly all lands, with a consequent increase in aridity and diminution of moisture-loving vegetation. This meant the great spread of grasses and a necessary adaptation to grazing habits on the part of such mammals as could do so, and the weeding out or extinction of such as could not. The widespread meadows also gave insect and bird life a more diversified habitat and therefore an evolutionary impetus.

Paleocene.—The formations lying between the undoubted Cretaceous and Eocene, whose true age has been debated, are called Paleocene. These include in the Great Plains region of the United States the formations known as the Fort Union, Puerco, and Torrejon, altogether some 1,000 to 2,000 feet of strata. The dinosaurs were apparently extinct and had been replaced by the archaic mammals (see below).

Eocene.—The Eocene period immediately followed the extinction of the great reptiles. Then nature began afresh to people the world with terrestrial animals, this time of the warm-blooded furry mammalian stock which had so long been held in check, for though they had existed during the Age of Reptiles their evolutionary progress was seemingly at a standstill. The first deployment of mammals gave rise to creatures which served fairly well but were limited in their potential mentality, among other defects, and from Eocene times an increasing value has been placed upon mental progress in the struggle for existence. These *archaic mammals*, as they have been called, underwent a brief career and were gradually replaced by the modernized forms whose brain power was capable of vastly greater development. By the close of the Eocene, the replacement was practically complete and but few survivors of the ancient mammals are extant.

Oligocene, Miocene, Pliocene.—During the Oligocene came the increasing aridity of climate which culminated in the Miocene, and with it the gradual elimination of browsing and the development of grazing types. The Miocene was the time of mammalian culmination, of both numbers and kinds. The Pliocene, with its increasingly hard conditions, prophetic of the glacial age, the formation of new land-bridges and the severance of others, was a period of great unrest. Many migrations occurred the world over, new competitions arose, and the weaker stocks began to show the effects of the strenuous life. One momentous event seems to have occurred in the Pliocene, and that was the transformation of the

precursor of humanity into man—the culmination of the highest line of evolution!

Pleistocene.—The Pleistocene was the final period of the Cenozoic, when, owing to continued elevation of the great continents, the Age of Ice was ushered in, with its long periods of devastating cold, separated by warmer interglacial times when conditions were less severe and the great ice sheets retreated into their northern fastnesses. The Pleistocene was a time of wholesale extinctions, when many races of animals were blotted out, but mankind, because of his superior mental attributes, was able to survive and rapidly took his place as the dominant form of life.

Psychozoic

With the final retreat of the ice, the Psychozoic era or Age of Man began, with the greater perfection of man's mentality and the assertion of his "dominion over the fish of the sea, and over the fowl of the air, and over the cattle, and over all the earth, and over every creeping thing that creepeth upon the earth," and the rise of world civilizations until their purging in the holocaust of the world's greatest war!

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PART II

THE MECHANISM OF EVOLUTION

CHAPTER VI

VARIATION AND MUTATION

All scientists and most other informed men are now convinced of the truth of evolution, both inorganic and organic: that out of simple beginnings, when in the course of ages the earth was fit for organic habitation, life began, and by a continual unfolding process there have come not only all of the marvellously adapted forms of animal and plant life which we see to-day, but those which Paleontology reveals to us and such as we know existed but of which no discoverable relics remain.

For our purpose, then, the *fact* of evolution is taken *ab initio,* without argument, together with the assumption that all organisms which do exist or have existed are blood-related, though the degree of relationship varies from the nearest to one inconceivably remote. But while the fact of evolution may be accepted as true, the ways and means whereby it has been brought about are not so evident and have given rise to endless argument and discussion. These are the *factors* of evolution; what they are, by whom advocated, the arguments offered for their acceptance, and their plausibility are the chief subjects of our present study.

Summary of Factors

To summarize the various factors which have been proposed, the list is briefly presented here; the arguments will be given later.

Variation is the first and most fundamental evolutionary factor, in fact, the causes of variation are among the prime causes of evolution itself. Variation, the fact that no two organisms or parts of organisms are precisely alike, no matter how closely related, is a commonly observed phenomenon, and admits of no argument whatsoever, as it is an established truth which any one, within the limits of his opportunities, may demonstrate for himself. It is the progressive factor in evolution, for without variation no change could occur and evolution would be impossible.

Heredity.—The second fundamental factor is heredity, the conservative factor in evolution, that which, when variation has

given rise to a new character, causes it to persist. Evolution is the change produced in a *race* of organisms; the mere variation of the *individual*, no matter how profound or how beneficial it may be, is not evolutional until it can be handed on to the offspring, and this is the function of heredity. Heredity, therefore, is as essential a basic factor as variation itself, and is just as fully established a fact; but, like variation, there are points concerning it, especially as to the means whereby a variation becomes heritable, which are still among the unsolved problems of our science.

Segregation.—Another essential basic factor is isolation or segregation, the physical or biotic barrier which prohibits promiscuous interbreeding. Forms with similar variational tendencies should interbreed to perpetuate them, and dissimilar forms should not, otherwise the new variations would be swamped and unless they were of dominant character would straightway disappear. Isolation, while not of such fundamental importance as variation or heredity, nevertheless stands forth as an extremely necessary adjunct to the evolutionary process.

The first means whereby segregation is accomplished is *physical*, as in the instance discussed under geographic distribution—the Galapagos tortoises (page 42)—or the land snails of Tahiti and Hawaii. A second form of isolation is *biotic*, either physiologic, where, due to actual structural differences, mating is either a physical impossibility or the germinal elements fail to combine, or if they do the resultant offspring either does not develop or is in itself sterile and cannot procreate; or the impediment may be a psychologic one. This seems to be largely a matter of instinct and is of undoubted importance in nature, as it is with humanity. It may be largely responsible for the purity of such races as the Hebrews, although even under the best of conditions it is not universally effective.

These fundamental factors are admitted by all, but there are other causal factors advocated originally by Charles Darwin which may or may not be true, as all students of evolution do not accept them. They are as follows.

Natural selection is the great Darwinian factor, and is to-day held by certain writers, notably those of the so-called Neo-Darwinian school, of which the German savant August Weismann was the leader, to be almost the only factor to be considered. Natural selection determines what variational lines shall persist and what

shall be eliminated, and, according to the Neo-Darwinian school, acts upon small uncontrolled variations, occurring in any conceivable direction of change. Nature either weeds out those forms in a race whose variations are out of harmony with environmental needs, allowing the others to survive and hand down their adaptive changes to offspring, or it selects the fitter to survive, or it may use a combination of the two.

Saltation.—Not all authorities, however, accept natural selection as an important factor, for the School of Saltationists, headed by the celebrated Dutch botanist, Hugo de Vries, believe that new species arise by sudden marked changes appearing in the offspring of normal parents. These large changes or variations were called mutations (Lat. *mutare*, to change) (De Vries) or saltations (Lat. *saltare*, to leap). Saltationists believe that natural selection therefore has nothing to do with species-forming, but only in a general way with descent control, that is, keeping the successive generations of a species true to type when once it has been formed.

Still a third, the Compromise School, believes that natural selection is important both in species-forming and descent control, but is not the "Allmacht" which the Neo-Darwinians would have us believe. They recognize the existence of various other factors working simultaneously with selection to effect the evolutionary change.

Sexual Selection.—Still another Darwinian factor is sexual selection, the means whereby Darwin sought to explain the existence of what are known as the secondary sexual characteristics among animals. As we shall see, this is the most doubtful factor of all of those advocated by Darwin and has little acceptance to-day (see page 139).

Variation

The basic prerequisite to evolution is undoubtedly variation, which together with heredity may be regarded as an undeniable fact. Therefore, as has been said, the cause of variation must be a contributory cause of evolution itself. But not all variations are alike, and only certain ones, apparently, are heritable, hence it is necessary to understand quite clearly what sorts of variations exist, since those that can not be inherited can have no part in the evolution of a species, as they concern only the individual and not the race.

Sorts of Variations

Variations may be grouped into three pairs of contrasting sorts—germinal or acquired, continuous or discontinuous, determinate or indeterminate—six in all. A given variation belongs in each of the three groups but must be either one or the other of the contrasting sorts within the group, as they are mutually exclusive. The first group is based upon the nature or cause of occurrence. It includes:

(1) **Germinal variations are intrinsic,**—such as arise in the germ-plasm itself due either to *recombinations*, which owe their origin to new groupings of the germinal factors or genes; or to *mutations* which result from relatively radical alterations in the gene complex. Changes due either to recombinations or to mutations are of course manifest only in the animal or plant body, the soma, and do not depend on external conditions for their origin. Such conditions may impede or arrest their development but cannot cause them. Often these mutations cannot appear until later in life, as, for example variations in adult size and proportions. They may appear at any period from the beginning of embryonic life to the death of the organism.

(2) **Acquired or somatic variations or modifications,** which are imposed upon the organism during its lifetime and are due to *extrinsic* influence. Under which of these two heads a variation should fall is often almost impossible to decide except by experimental work, and sometimes not then, but the difference is of fundamental importance, for germinal variations only can be inherited by the offspring.

Examples of germinal variation are the occasional occurrence of supernumerary digits in man, the domestic cat, the horse, and other forms, for they can not be due to accident or to any external influence and are occasionally inherited through several generations. On the other hand, the loss of a digit in man through too close proximity to a circular saw would certainly be an acquired characteristic and long series of experiments have proved conclusively that such variations are without the pale of heredity.

Another example which occurs normally in nature would be the hive bees (*Apis mellifica*), in which the sex distinction between the workers and queens is an acquired variation, while that between drone and queen or worker is germinal. The queen is impregnated

but once, the male elements being stored in the seminal receptacle, and used one at a time for the subsequent fertilization of the eggs. The workers build two sizes of cells in the brood combs, in the larger of which the queen lays an unimpregnated egg, while that laid in the smaller cell is fertilized at the time of laying. From the unfertilized egg there arises, invariably, a drone or male bee, while the fertilized egg produces a potential female. Hence the difference between male and female bee, depending as it does upon impregnation or not, is germinal. The ultimate fate of the impregnated egg is subject to the control of the workers, for while the vast majority of the eggs remain within the small worker-cells and, being fed upon a meager and comparatively innutritious diet, develop into workers—the so-called neuters, which are in reality undeveloped females—a select few have their cells enlarged at the expense of the surrounding ones and are fed upon highly nutritious "royal pabulum" and ultimately develop into mature females or queens. It is said that even after three days of larval life, the humble worker, like the beggar maid of King Cophetua, may become a queen. Thus this variation, being imposed upon the animal during life, is an acquired one.

Indeterminate and Determinate.—Variations may be further classified according to direction of occurrence, as (3) indeterminate, those fortuitous variations which are not subject to any law but occur in any conceivable direction of change; or (4) determinate, controlled by some unknown influence and confined to certain definite lines or directions of change, usually in an adaptive direction. Of the first of these two contrasting types there is no doubt, and they are the variations upon which the Darwinian factor of natural selection is supposed to operate. Illustrations are legion, as the comparison of any group of related organisms will show a variation of size which embraces every dimension of space and combination thereof.

Of determinate variations we are not so sure; some claim that they have no real existence, that there is no such tendency to vary always in a given direction in successive generations, while others consider these variations, which they call orthogenetic (Gr. ὀρθός, straight, and γένεσις, generation), *the* important ones in evolution.

What is apparently an example of determinate variations is that given by Kellogg, who described in 1906 the gradual but obvious change from one dominant type of color-pattern to another in the

leaf-eating beetle *Diabrotica soror.* It is apparently proved that such change is not explicable on a basis of intra-specific selection, nor can it be interpreted as a direct ontogenetic (pertaining to the individual) reaction in each succeeding generation to changing climatic conditions. It is believed to be an example of definitive orthogenetic variation.

Many paleontologists think they see repeated instances of orthogenetic variation, since they are, as a rule, so deeply impressed by the adaptive nature of the evolutionary process and the definitiveness of its direction, that they cannot believe the restraining or selective action of the environment is enough to keep the breed true; for example, the sure way in which the cusps of the teeth in ungulate animals appear in the course of time, so that one can predict the ultimate tooth pattern at the end of an evolutionary series with fair assurance. The rhinoceroses, on the one hand, and the totally unrelated coney, *Hyrax*, on the other, have teeth so similar that Roosevelt calls attention to the fact in his *African Game Trails* (see Fig. 9). This is an instance of *convergence*, which is often the result of what is apparently orthogenetic variation. The overgrown antlers of the Irish deer or the tusks of the Jefferson mammoth (see Chapters XII and XXXV) which in each instance seem to be so far beyond the point to which natural selection would carry them, may be considered as further instances of this form of variation.

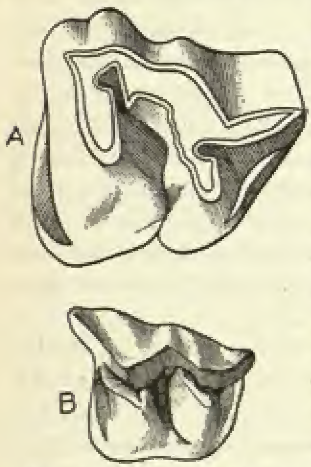

FIG. 9. — Teeth of (A) rhinoceros (*Cænopus* sp.); and (B) coney (*Hyrax capensis*), much enlarged. (After Scott, and Osborn.)

Continuous and Discontinuous.—Variations may also be classed according to difference of degree, as (5) continuous, that is, small, abundant, and occurring in graded series. These, if also fortuitous, are the so-called Darwinian variations or fluctuations, to be acted upon by natural selection. They are generally quantitative rather than numerical variations, and the increment of change between successive generations is extremely slight.

In contrast to the continuous are the (6) discontinuous variations, which are mostly large and rare. They are also known as sports or saltations (see page 90), although the distinction between them and the continuous is only one of degree, as the two sorts merge into each other.

The great mass of variations come under the head of continuous, the discontinuous ones being relatively rare, although many such have been recorded, as for example the numerous instances of variation from the standard number of digits in vertebrates. In mankind, six, seven, or even eight fingers to the hand have been observed (see Fig. 10), while the doubling of the foot has brought the number of toes as high as nine on a side. Cattle and horses sometimes show multiple digits and, on the other hand, pigs with the two median toes united into one perfectly formed digit, the so-called, solid-hoofed pigs, occasionally occur. Sheep sometimes show four horns instead of two, but the peculiarity is that instead of having one pair behind the other as in the normal four-horned antelope (*Tetracerus quadricornis*) the horns always stand in a single transverse series across the skull. One family of goats on an isolated farm near Bozen has four horns which have been inherited for many generations (Bateson).

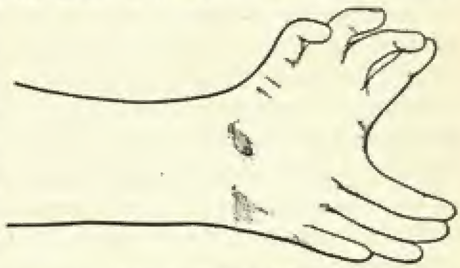

Fig. 10.—Eight-fingered hand, *Homo sapiens*, female. (After Murray, from Bateson.)

All of these are instances of meristic (Gr. μέρος, part) or number variations and are likely to occur wherever any structure is repeated in numerical series: in the number of segments of worms and arthropods, or in the vertebral column, ribs, and muscles, and in the number of appendages. Radially symmetrical forms such as sea-anemones and starfish also exhibit meristic variation and it frequently occurs among plants, especially in the flowers or leaves, as in the four-leaf clover.

Other instances of discontinuous variations are not of this numerical sort but are mutations of color, form, and size. Such, for example, are the famous new saltations of Lamarck's evening primrose (*Œnothera lamarckiana*), which breed true and gave rise

to De Vries's theory of the origin of new species by brusque saltations. Some of these vary from the original in size, one is a smooth-leafed form with a more beautiful foliage, and so on. Another example is that of the short-legged ram which suddenly appeared in Massachusetts in the year 1791. This ram proved to be a potent sire, capable of handing on his peculiarity to his progeny, and thus was the founder of a breed of so-called Ancon sheep whose principal virtue was their inability to jump fences due to the brevity of their limbs; with the introduction of the more desirable merinos, breeders allowed the Ancon sheep to disappear.

Causes of Variations

The causes of acquired variations are apparent, for every modification which the organism undergoes in its lifetime in response to any external condition whatsoever comes under this head. The influence of abundance or scarcity of food in giving the animal a greater stature or one less great than that of its brethren, the influence of heat, cold, omnipresent enemies, or even the absence of exacting conditions: all these make themselves felt upon the individual in greater or less degree, but, as has been emphasized, this individual adaptation, however interesting it may be, is *not* evolution. Therefore in our inquiry into the subordinate factors of evolution, it is not the cause of *acquired*, but of *germinal* variations with which we are concerned.

Causes of Germinal Variations.—As these variations are highly important raw material of evolution, it is at once apparent that the cause or causes which produce them are of fundamental importance as prime movers of the whole process. Our ignorance of these causes is profound, nevertheless the following ideas concerning them are worthy of record.

First, the inherent tendency to vary. This does not, however, state a cause but merely a fact and really begs the question. The reverse of the statement—the almost absolute impossibility of two organisms being alike—is perhaps the better way to express it. When one thinks of the marvellous complexity of protoplasm, consisting as it may of sixteen or more elements with the atoms numbering thousands, held in an atomic structure so complex that the chemist cannot express it graphically, as he can simpler compounds such as water, he sees how remote is the possibility of any two particles of protoplasm being precisely alike. Furthermore

the organism, no matter how simple, is made up of countless molecules, and these are in a continual state of chemical change due to energy traffic. How then can one possibly expect coincidence of detail in any two organisms, no matter how close their relationship? The amazing thing is not that they differ, but that they are so much alike!

Second, dual or biparental parentage (amphimixis) has been given as a principal cause of variation. That which is actually handed on to the next generation is the germ-plasm (see Heredity, p. 95) derived in part from each parent. This in itself is a highly complex material, consisting of chromosomes which, in man for instance, number 48. During the process of maturation of the germ cells, ova and spermatozoa, the number is reduced to 24. These are combined in the process of fertilization so that the number of chromosomes in the initial cell of the embryo is once more 48. The process may be likened to two miniature packs of cards, each of which is elaborately shuffled, one-half the cards rejected, and the remaining halves combined into a new pack. This gives rise to an enormous number of possible re-combinations. If the packs contain 48 cards, instead of the normal 52, to correspond with the human chromosomes, the number of possible permutations will be 16,777,216, and for the average germ capacity during the sexual life of a pair of parents the total number of different combinations of fertilizable ova would be 300,000,000,000,000 (Dorsey from Thomson). No wonder the children of a family differ!

Third, actual observation shows that variation also occurs where there is but one parent, as in the Protozoa, where offspring are produced by the division of the mother cell into two daughter cells. Also in higher animals where the offspring come from a virgin mother without the intervention of the male (parthenogenesis), as in many insects—bees, plant lice, and the like; but here again there is the same process of halving the pack with the maturation of the ovum, giving opportunity, although not mathematically so great, for re-combinations in the offspring. In the protozoan *Paramecium*, Woodruff has observed a periodical reorganization of the nuclear apparatus (endomixis), which in some way seems to rejuvenate the race. Here again there may be an opportunity for new chromosome combinations to emerge.

The second and third might account for germinal variations

which are the result of re-combinations of ancestral characters appearing in the offspring, but there are also the mutations, which are due to fundamental changes in the germinal constitution itself. To account for these our first statement might apply in part.

Another idea is that, in spite of the insulation of germ-plasm from extrinsic influence, nevertheless some of the more deeply saturating results of the ever varying environment may act directly on it and so bring about heritable change. This has been definitely shown by X-raying the germ-plasm.

A new line of research, which is yet far from complete, is the study of the endocrine or ductless glands, which are already known to have a profound influence upon individual development, both mental and physical, including that of the secondary sex characters. These glands do not form secretions in the sense that the salivary and other digestive glands do, but are connected only by the blood stream, into which are poured under proper stimulus the hormones or chemical messengers which they manufacture. These hormones are picked out of the blood stream by the appropriate organs and upon them exert a powerful influence. They pass through the reproductive glands as readily as elsewhere, and it is reasonable to suppose that certain of these hormones may react upon the germ cells as well as upon the body cells. This may prove to be a mechanism whereby external influence is exerted on the most intimate parts of the organism.

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CHAPTER VII

HEREDITY

With heredity again, as with variation, we are dealing with a fact; the laws of heredity and whether or not certain characters are heritable, however, are subjects for debate. Heredity is defined by the Century Dictionary as the principle or fact of inheritance, or the handing down of physical and mental characteristics from parent to offspring, regarded as the conservative factor in evolution, opposing the tendency to variation under conditions of environment. Heredity may also be defined as the rule of persistence among organisms, each organism being likely to resemble its parents; and as "the organic relation between successive generations which secures persistence of characteristics and yet allows new ones to emerge" (Thomson).

By some writers heredity is considered the force which compels the resemblance; by others the process whereby the offspring comes to resemble its immediate ancestry. Of course, while partaking of the nature of each parent to a certain extent, the organism through them partakes also of the nature of its grandparents and so on back in ever diminishing degree.

The problem of inheritance, especially the means by which it is brought about, is one of the most interesting in Biology. Formerly the fact of inheritance was considered self-sufficient; now inquiry into the mechanism of heredity has thrown much light upon the problem of evolution itself.

Physical Basis of Heredity

The mechanism of heredity has been investigated by a great number of workers, some of whose results follow.

Encasement Theory.—One of the older, but now abandoned, ideas was set forth in the preformation or encasement theory, which supposed that the germs of all future generations were encased, one within the other like Chinese boxes, in the progenitor of the race and were successively developed into perfect individuals with each arising generation. Thus Mother Eve, taken as the

ancestress of all mankind, was estimated to contain no fewer than two hundred million homunculi, an assumption that spoke well for the imagination of the older writers.

Darwin's Pangenesis Theory.—Darwin realized that his doctrine of natural selection lacked completion if he merely accepted the fact of heredity at its face value without trying to learn in what way mental or physical traits or new variations got into the egg or sperm and thus were borne on to the next generation. He therefore devised the theory of pangenesis (Gr. πᾶς, all, and γένεσις, generation), according to which every cell of every tissue and organ of the entire body produces minute particles called gemmules, which in each instance partake of the nature of the cells producing them. These gemmules may circulate throughout the entire organism but finally congregate in the reproductive products or in buds, so that each germ cell or each bud (asexual) capable of giving rise to a new individual would be in a sense a miniature replica of the parents' body and would thus be capable of developing into the same kind of a body even in minute detail. Darwin thought that sometimes certain of the gemmules might lie dormant for several generations and then develop, bringing out in an individual its ancestral (atavistic) traits. If this theory of gemmules were true, it would lead to the acceptance of the teaching of Lamarck or even of Buffon, because under such circumstances the inheritance of acquired characters gained by the parent during its lifetime would be entirely feasible, for such modification could be impressed upon the germ cell as readily as could the variations which we call germinal.

Later research, however, proved that such a theory has no basis in fact and biologists soon began to search for a substance which could be a physical basis for heredity just as the protoplasm which makes up the bulk of all organisms is the physical basis of life, and while several biologists were convinced that there was such a substance, it remained for August Weismann, for nearly fifty years professor in the University of Freiburg, to identify and demonstrate its existence.

Weismann's Germ-Plasm Theory.—Weismann's germ-plasm theory was published in 1892 in a volume called *Das Keimplasma*, wherein he brought together the accumulated observations of the numerous contemporary students of cell biology and utilized them for the development of his somewhat speculative theories. This

volume Crampton calls "an immortal foundation for all later work on inheritance." The essential principles of the germ-plasm theory are as follows (see also Fig. 11).

Weismann divided all the substance of an organism into two parts, the germ-plasm and somatoplasm (Gr. *σῶμα*, body, and *πλάσμα*, anything formed or moulded), the former, the protoplasm of the germ cells, being the actual vehicle of heredity, while the latter, which constitutes the remainder of the plant or animal body, was not. In reproduction a portion of germplasm is derived from each parent, the paternal sperm and maternal ovum, as the case may be, each of which has an equivalent share in the inheritance. These combine to form the fertilized egg. When the egg divides in the first or subsequent cleavages each daughter cell receives an equal share of germ-plasm, and this holds true for all cells which go to form the adult body. None of the somatic cells, however, has any share in subsequent generations but only the germ cells which are derived directly from the original egg. It follows, therefore, that there is a continuous stream of germplasm from generation to generation, to which the somatic cells, which are sister products from the original egg, contribute nothing. Hence only those mutations which are germinal in their origin can possibly be handed down, and, as the hereditary stream of germ-plasm is already set apart before the adult body is in use, one cannot see how any modifications impressed upon the latter through use or

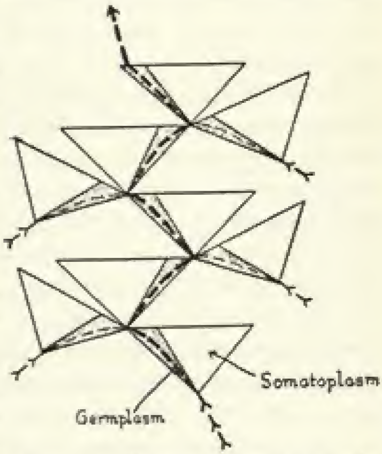


Fig. 11.—Diagram to illustrate the continuity of the germ-plasm. Each triangle represents an individual made up of germ-plasm (dotted) and somatoplasm (undotted). The beginning of the life cycle of each individual is represented at the apex of the triangle in which germ-plasm and somatoplasm are both present. As the individual develops, each of these component parts increases. In sexual reproduction the germ-plasms of two individuals unite into a common stream, to which the somatoplasm makes no contribution. The continuity of the germ-plasm is shown by the heavy broken line into which run collateral contributions from successive sexual reproductions. (After Walter.)

disuse, or extrinsic adaptations to the environment, can possibly become a part of the organism's heritage.

In certain of the Protozoa not only is the germ-plasm handed down, but the entire body of the organism may be divided between the offspring. Yet other Protozoa, which reproduce by budding, give up only a portion of their nucleus and cytoplasm to their children, and the same thing is true of all organisms which reproduce asexually.

On the other hand there are plants and animals, the hot-house *Bigonia* and the earthworm for example, in which purely somatic cells have the power to regenerate a complete organism, including reproductive organs and germ-plasm. In the earthworm the reproductive organs reside in the anterior segments and yet, no matter where the worm is cut asunder, if enough of the tail remains, it will reproduce the entire organism, including the reproductive bodies, with all of its specific hereditary details. This shows that "we must postulate at least a potential supply of the germ residing in the somatic tissue which can make good the definitive germ cells when they are lost. . . . It is a fact that there is a continuity of germ-plasm, whether the germ cells are set aside early in individual development, or later by the transformation of relatively undifferentiated typical somatic cells: this is really the crux of the question" (Woodruff). True freedom from all outside influence in these circumstances would be little short of marvellous, and yet that is what we are led to believe.

Latent and Potent Qualities.—The sum of the inheritance of any organism contains many qualities not all of which are externally manifest in the individual. This is especially true of two contrasting qualities which are mutually exclusive; for instance, a child, one of whose parents is tall and the other short, may have an ultimate stature which is in a sense a compromise between the two, or on the other hand he may be tall and yet nevertheless have the power of transmitting to his offspring the short stature which he inherited along with his tallness, but which was latent within him. The qualities which are manifest are therefore *potent* or *dominant*, while the invisible ones are *latent* or *recessive*. The latter may be none the less real in heredity. A more remarkable instance is found in the drone bee once more, which, as we have seen, comes from an unfertilized egg and therefore has no father but only a mother. Nevertheless all his qualities of maleness, his

reproductive organs, size, and any other characteristics whatsoever which distinguish him from the female, including his inborn aversion to labor, are inherited through his mother, the queen-bee. She therefore had these qualities present in every one of the germ cells which she inherited from her father; but those germ cells which are fertilized, in other words, those which have the male qualities latent and the female dominant, receive the stimulus which brings this about from the male. Therefore if the bee has no father, it exhibits fatherly qualities; if it has a father, it does not.

Atavism.—This leads us to the problem of atavism (Lat. *atavus*, an ancestor, from *avus*, a grandfather) or reversion to ancestral type. Under atavism have been included what have been called three very different things but which seem to be largely differences of degree. They are:

1. *Family atavism.* The transmission, within a family, of individual characters in latent condition for several generations and their sudden reappearance; for example, red hair in a child, which the immediate parents or grandparents do not show, but which was in evidence several generations back.

2. *Race atavism.* The more or less regular reappearance in a race of characters of another race, from which the first may have been derived. Such, for example, are the instances of the profuse development of hair on the face and body which occasionally occurs in man, as in the Russian "dog man," Adrian Jeftichjew (see Fig. 252).

3. *Atavism of teratology* (Gr. τέρας, wonder, monster). The appearance in a race of abnormal characters which, however, are normal in other supposedly ancestral races. Exemplifying this are the external hind limbs of which a single recorded instance occurred in a humpback whale taken off Vancouver. The ancestral terrestrial *atavus* of the whales undoubtedly had these structures, which were gradually lost among other adaptations to aquatic life (see Chapter XX). Fistulæ, or permanent abnormal openings of the neck, which sometimes occur in the human subject, have been considered as relics of the ancient gill-clefts of our piscine ancestry (see Chapter XXXIX).

In summation it may be said that "less marked cases set down to atavism may be instances merely of normal regression. Many cases of more abnormal structure, which are really due to abnormal embryonic or post-embryonic development, are set down to atavism,

as, for instance, the cervical fistulæ [mentioned above] . . . It is also used to imply the reversion that takes place when domestic varieties are set free [to interbreed indiscriminately] and when species or varieties are crossed. Atavism is, in fact, a misleading name covering a number of very different phenomena" (*Encyclopedia Britannica*).

Telegony (Gr. τηλέγονος, born far away).—There is a very widespread feeling among breeders of domestic animals, especially of the finer strains, that the first male bred to a female will influence not only his own offspring but subsequent young by another sire. Up to the end of last century Lord Morton's experiments with a male quagga and a young chestnut seven-eighths Arabian mare were regarded as affording strong evidence of this theory. These experiments were repeated as accurately as possible in 1899 by J. C. Ewart. The initial one was the impregnation of a mare, "Mulatto," by a Burchell's zebra. The offspring, "Romulus," resembled the richly striped Somali zebra more than his sire. Later "Mulatto" was bred to a pure Arab stallion, but while the foals showed traces of stripes, they were decidedly less suggestive of zebras than were pure-bred foals of a near relative of "Mulatto" which had never seen a zebra. Ewart considers the evidence inconclusive, and believes that the apparent instances are due to other factors.

It is evident that what is called telegony does not actually exist. In highly bred strains of dogs, for instance, there are repeated occurrences of reversion to an inferior type which require constant care on the part of the breeder to eliminate, in order to breed only from the better examples.

Prenatal Influence.—There is a widely held belief that in mammals a special additional formative influence is exerted by the mother in the period between conception and birth. Maternal impression, so-called, does not refer to the results of good or poor nutrition, which are discussed below, but to the development in the unborn young of definite anomalies such as birthmarks and the like. While instances are numerous, they have never been given accurate scientific research and are still open to question; nevertheless, many people believe in prenatal influence and the belief is very old, as the first recorded instance known to me is in Genesis XXX, 32–42, dating back to the time of the patriarch Jacob, about 1730 B.C. Jacob was to receive as his share of Laban's

flocks and herds "all the speckled and spotted cattle, and all the brown cattle among the sheep, and the spotted and speckled among the goats," while Laban was to retain such as were not so marked. So Jacob "took him rods of green poplar, and of the hazel and chestnut tree; and pilled white streaks in them, and made the white appear which was in the rods. And he set the rods which he had pilled before the flocks in the gutters in the watering troughs when the flocks came to drink, that they should conceive when they came to drink. And the flocks conceived before the rods, and brought forth cattle ringstreaked, speckled and spotted." Jacob was shrewd enough, however, to put the rods before the eyes of the stronger cattle, "but when the cattle were feeble, he put them not in: so the feebler were Laban's, and the stronger Jacob's."

Transmission of Parental Conditions.—One thing which must be distinguished very clearly from heredity is the transmission of characteristics which are not those normal to the race but those peculiar to the parent, such for instance as the malnutrition of the embryo due to the weak or impoverished condition of the mother. Heredity hands down qualities of the parents as they should be, transmission as they are; the one is concerned with the nature, the other with the nurture of the individual. In breeding, the potentially best is often better than the actually best, as an old race horse sire will produce speedier colts than a young and vigorous cart horse. Nevertheless, the feebleness of either parent through disease or debauchery may produce offspring with so heavy a handicap that they are never able to overcome it and cope with others of potentially inferior stock. Insufficient nutrition both before and after birth may partially neutralize the most vigorous inheritance.

Sex Determination.—The problem of sex determination is an interesting one for which many theories have been advanced, but the fundamental differences in sex are not so great as might be imagined, as the organs of the one are often represented as rudiments in the other, the differentiation coming about mainly through division of labor between male and female in the production and nutrition of offspring.

The actual determination of sex resides in the germ itself and is established at conception; the development of sexual characteristics, on the other hand, may well be due to the influence of certain hormones secreted by the endocrine glands. The latter derange-

ment sometimes gives rise to sexual anomalies, such as pseudohermaphroditism in higher vertebrates, even in man. Occasionally there occurs true hermaphroditism (Gr. Ἑρμῆς, Hermes, and Ἀφροδίτη, Aphrodite), that is, a combining of the sexes in one individual. Among animals this is rare and is almost invariably found in sedentary or semi-sedentary types. For example, the European oyster is hermaphroditic, while its American ally is not. Barnacles, sedentary Crustacea, are often bisexual, and sometimes there may be seen within the body of the hermaphroditic female a small, so-called complemental male, evidently in process of elimination from the race. The snail and earthworm, which, though not sedentary, have very limited powers of movement, also have the sexes combined, while in plants separate sexes are the anomaly, hermaphroditism being the rule. Among invertebrates the proportion of the sexes varies enormously; among vertebrates, on the other hand, they are generally nicely balanced. In the hive bees, as we have seen, unfertilized eggs invariably produce males, whereas among aphids parthenogenesis gives rise to females only until autumn, and then to both sexes, while the fertilization of the winter egg, as in the bees, produces females only. Here the appearance of males—and the same is true of wasps and many other insects—is a harbinger of cold and inclement weather, and may sometimes be postponed by artificially continued uniform conditions. For example, the scale insects (Coccidæ) found in a state of nature normally produce the males toward the end of the growing season, and this is also true of some types resident upon hothouse plants (*Pulvinaria* sp.). On the other hand, certain hothouse species far from their native habitat have been observed for years without the discovery of a single male.

Homologies and Analogies.—The distinction between homologous organs which have the same structure and origin, in other words, such as are morphological (Gr. μορφή, form) equivalents, and analogous organs which have a similar use or function but which may not be historically identical is often of the utmost importance. Homologous organs imply blood relationship on the part of their possessors and are therefore the basis for classification. Analogous organs, on the other hand, while they necessarily have the same function, may have their origin in very unlike structures and may be very misleading to the systematist. Such, for example, are the various types of wing whereby at least four different

groups of animals, three vertebrate and one invertebrate, have attained true flight. In the vertebrates, the birds, bats, and the extinct pterodactyls have each independently developed a wing, but in every case it is the modified fore limb equivalent to the arm and hand of man. Hence the wings of bat and bird and reptile are both analogous and homologous, as they are historically the same organ and also have the same function. The wings of the insect, however, are not the same structure at all, but are modified out-pushings of the body-wall which have become expanded into thin membranous plates, stiffened with veins and ribs,

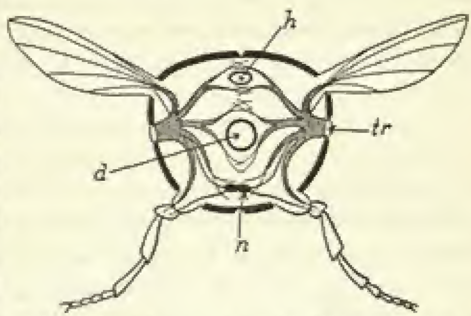


FIG. 12.—Section of insect, showing wings. *d*, digestive system; *h*, heart; *n*, nervous system; *tr*, tracheal system. (After Packard.)

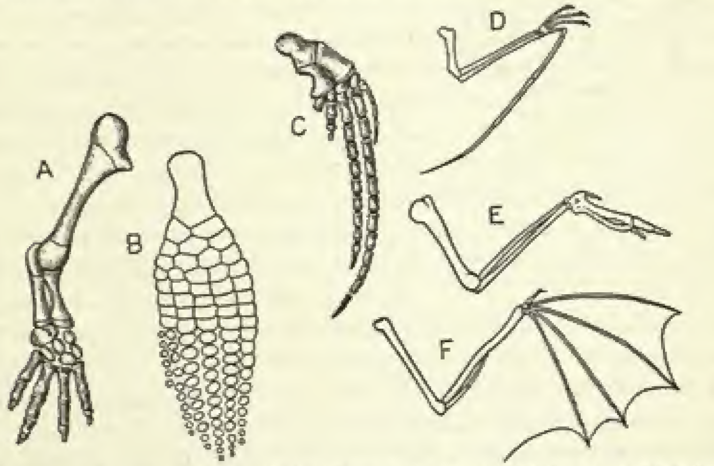


FIG. 13.—Vertebrate fore limbs (homologous). A, *Necturus*, a primitive salamander; B, *Ichthyosaurus;* C, *Globicephalus*, a dolphin; D, pterodactyl; E, bird; F, bat. (After Wilder.)

movably articulated to the body and endowed with muscles to sustain their owner in the air. Hence the wing of the insect is analogous to those of the bird and bat, but not their homologue at all. (See Fig. 12.)

This matter of homologies may be carried further, for not only do the fore limbs of forms so remote in habits and habitat as a salamander, ichthyosaur, bird, and whale (see Fig. 13) agree in being the homologues of one another as a whole, but the individual bones and even the principal muscles of one limb are homologous with those of another.

Classification, which, as has been said, should show true phyletic relationship, is based upon the resemblances and dissimilarities of homologous structures.

Vestigial Organs.—Vestigial organs are such as are not fully developed, and are to be contrasted with rudimentary structures which are in process of evolutionary growth and thus are progressive, whereas the vestigial organs are retrogressive and are tending toward diminution and ultimate loss. Rudimentary horns are often observed on the head of fossil ungulates such as titanotheres and rhinoceroses, whereas the splints on either side of the cannon-bone of a horse's foot are vestiges of formerly useful lateral toes. The vestigial organs are therefore of historical importance and would not exist, especially where their old-time function has entirely ceased, were it not for heredity.

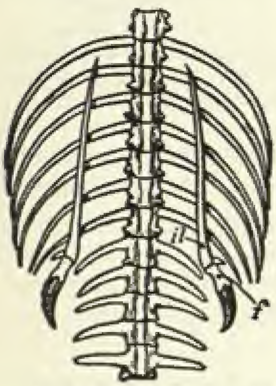


Fig. 14. — Vestigial hind limbs of python. *f*, femur or thigh; *il*, ilium or hip bone. (From Romanes' *Darwin and After Darwin.* Copyright, Open Court Publishing Co.)

Of such are the vestigial hind limbs seen in the python and other related snakes. Externally they are mere spurs on either side of the vent, internally they are seen to contain several of the bones normal to a fully formed limb, ilium, femur, tibia, and claw (see Fig. 14). Embryo whales generally exhibit the coat of hair of their ages-vanished forebears, and also, as Kükenthal has shown, the relics of hind limbs as well developed buds. At birth, however, the hair has been shed except for a few bristles about the lips and all external trace of hind legs has gone, there being only a few bones, as in the python, buried deep within the mass of the creature's flesh (see Chapter XXXIV).

Mankind, according to Wiedersheim, has no fewer than 180 such

relics, which will be discussed somewhat at length in Chapter XXXIX.

Atrophy of Parts.—Atrophy of parts, which results in these vestiges, has been variously accounted for, the three or four principal theories being as follows:

1. *Panmixia* (Gr. πᾶς, all, and μῖξις, mixing) or cessation of selection, the organ being no longer held up to a high degree of efficiency. Organs once useful, from change of environment or of habits are no longer of value, so that natural selection ceases to act upon them, and animals born with the organ somewhat defective or in a condition below the average would not necessarily be killed off in the intra-specific strife and would therefore be as likely to mate and keep on producing offspring as those with the organ of average or better than average development. Panmixia would obviously lead to a loss of high condition on the part of the organ, but how far the latter would degenerate and whether cessation of selection would ever cause it entirely to disappear, as the limbs of most serpents have, is open to serious question. This leads us to the second possibility.

2. *Reversal of selection.* Of this factor there can be little doubt, and it may well work in connection with panmixia, when a useless organ becomes a burden, to complete what the latter has begun. This theory postulates a change of condition or habit under which an organ previously beneficial may become actually detrimental to the animal. It differs from cessation of selection, which implies that the structure is no longer of selection value, hence its presence or absence is entirely immaterial. Here the absence of the organ is to be desired, therefore it is of negative selection-importance and not merely an indifferent thing. A very graphic instance wherein reversal of selection has been operative is that of the wingless beetles found on certain oceanic islands. In Madeira, for instance, there are 393 species of insects which are peculiar to the island. Of these 178 species cannot fly. The latter could not have reached the island in their present flightless state, so that the loss of flight is a local evolution (Scott). The inference is that while in a wide environment wings are so distinctly advantageous that natural selection would tend to strengthen them toward greater and greater perfection, in a small islet they would become a distinct menace, often causing their unlucky possessors to be swept overboard and drowned, and though the laws of chance

would operate as usual, nevertheless in the long run the individuals with the strongest powers of flight would be placed in the greatest jeopardy. Hence natural selection in opposition to its usual results would weed out what in most conditions would be the fitter, leaving the less fit to survive and reproduce their kind. It is not, therefore, a reversal of the *process* of natural selection, but a reversal of its *results* due to diametrically opposed conditions.

3. *Inheritance of the results of functional disuse.* This was apparently the simplest and most logical way to account for the atrophy of parts in evolution until Weismann's epoch-making work cast doubt upon it, for it is a well-known fact that, *with the individual*, use strengthens an organ while disuse causes it to weaken and partially atrophy. Witness the Hindoo fakirs who hope to acquire a state of singular holiness through the mortifying of the flesh. Some of them keep the arms raised permanently above the head, with a consequent shrinkage of muscle and stiffening of joint until the limb could not be used if they would. But as Weismann has shown, such modifications are those of the mortal somatoplasm and cannot, apparently, impress themselves upon the race. How then can this explanation account for the evolutionary atrophy of parts, unless there is still some factor of heredity which we know not of?

4. *Orthogenetic variations* (see page 87), if such exist, may account for the atrophy of organs as readily as for their increase, and for those who believe in determinate variation, the continued tendency to diminution, generation after generation, would suffice. If orthogenetic evolution has caused the continual strengthening and lengthening of the median toe of the ancestral horses, it can also account for the reciprocal shortening and weakening of the lateral ones until they ultimately disappear.

Summary. Thus cessation of selection might readily account for the initial reduction of an organ, but probably only to the condition of fluctuating around a mean, and would never cause its total atrophy. Reversal of selection under conditions where the organ is not only no longer useful but an actual menace would be a potent cause for its elimination. Inherited effects of disuse cannot be proved nor are determinate variations generation after generation of unquestionable occurrence. Consider the way the splint bones of the modern horse vary in every conceivable direc-

tion of change with no very marked tendency toward reduction since the Pleistocene.

Characters Which Are Not Heritable

Acquired Modifications.—Long observation has shown that certain variations among animals are not heritable. These are:

1. Acquired modifications due to disease, mutilation, use or disuse of parts, and changes due to the direct action of the environment upon the organism, such as the loss of color on the part of forms living in the dark.

2. *Characters peculiar to sex*, which are inherited, not by all, but by the appropriate sex. That is, the traits which are manifest, for in the case of the fatherless drone bee it will be remembered that as he inherited all of his traits, masculine and otherwise, through his mother, she must have borne all of the male characteristics within her but in latent condition. This is also shown by the fact that emasculated males are apt to show feminine traits, as with the domestic horse, wherein a gelding and a mare may make a very well matched pair, but not as a rule either a gelding and a stallion or the latter and a mare. It is not so much the feminine characters which the gelding shows as the lack of masculine which nevertheless are within the sum of its inheritance.

3. *Certain parental characters*, apparently not inherited, really have been received but lie in latent condition, to reappear in some future generation, as in the case of atavism.

Principles of Inheritance

Students of heredity have worked out a few definite principles of inheritance with which, under certain conditions, organisms seem to conform. The most interesting ones are Galton's laws (Francis Galton being a cousin of Charles Darwin), and Mendel's laws. The first of these, historically speaking are:

Galton's Laws.—Galton's law of *ancestral inheritance* was based upon two main sources: the study of the carefully kept pedigree book of the kennels of the Basset Hounds Club, whose records extended over a period of twenty-two years, and a study of inheritance in the British peerage, of which very complete genealogical records have been kept. Galton's statement is that "any organism of bisexual parentage derives one half of its inherited qualities from its parents (one fourth from each parent),

one fourth from its grandparents, one eighth from its great-grandparents, and so on. These successive fractions, whose numerators are one and whose denominators are the successive powers of two, added together equal one or the total inheritance of the organism, thus:

$$\tfrac{1}{2} + \tfrac{1}{4} + \tfrac{1}{8} + \tfrac{1}{16} + \tfrac{1}{32} + \tfrac{1}{64} + \ldots = 1\text{"}$$

This has been shown to be only a general approximation of the actual inheritance relations. Another consideration is due to the fact that each person has two parents and four grandparents, but beyond that the geometric progression may not hold, since even in a country like ours which draws its population from the four corners of the earth, each of the eight great-grandparents is not always a distinct person; for when parents are cousins, this number may be reduced to six, five, or even four instead of eight. Hence the share of each in one's inheritance is proportionately increased.

The law of *filial regression* states that the offspring of exceptional parents tend to regress toward mediocrity in proportion to the degree of parental exceptionalness, or, "On the average any deviation of the parents from the racial type is transmitted to the progeny in a diminished degree; the deviation from the racial mean being two-thirds as great as that of the parents" (Woodruff). This probably expresses a general truth, but whether or not regression will occur depends upon whether the exceptional characteristics of the parent are somatic modifications or actual germinal mutations. In the former instance there will be regression to a condition normal for the race; in the latter, there will be no regression.

Mendel's Laws.—That which we have come to call Mendelism was first discovered by an obscure Austrian monk, Gregor Johann Mendel, of Brünn, who was born in 1822 and died in 1884. Mendel wrote little but wrote that little with admirable clarity of thought; nevertheless it was apparently beyond the understanding of the "wise men" of his day. Mendel was in advance of his time, and the discovery of several biological principles then unknown, but now clearly understood, was necessary before a full understanding of his theories could be reached. Long after Mendel's death, in 1900, his laws were independently rediscovered simultaneously by three men, De Vries, Correns, and Tschermak, and it speaks highly for their chivalry that "honoring the all-but-forgotten monk, they

called the new-found laws Mendel's, rather than their own" (Castle). Bateson discovered the application of the laws to animals as well as to plants.

Mendel's laws were based upon a series of experiments carried on in the seclusion of the monastery garden upon pedigree cultures of peas (*Pisum sativum*) and other plants, and his results were published in 1865 in the *Abhandlungen* of the Natural History Society of Brünn. He found in the course of his experiments that the peas showed a number of pairs of contrasting characters, of which seven are recorded, one of each pair being dominant, the other recessive. These characters were:

1. Shape of ripe seed; whether round, or wrinkled.
2. Color of cotyledons; whether yellow, or green.
3. Color of seed skin; whether various shades of gray and gray-brown, or white.
4. Shape of seed pod; whether simply inflated, or deeply constricted between the seeds.
5. Color of unripe pod; whether green, or yellow.
6. Whether the flowers are arranged along the axis of the plant, or are terminal and form a kind of umbel.
7. Length of stem, whether dwarfed or tall.

The results of a large number of crosses showed but one only of each of these characters in the offspring in the first filial generation, proving that in each pair one character was dominant and the other recessive. By letting the cross-bred peas fertilize themselves, Mendel raised a second filial generation in which the proportion of dominant to recessive characters was with very considerable regularity in the ratio of three to one. In other words, the proportion in the offspring of cross-breds was approximately 75 per cent dominant and 25 per cent recessive. These were again self-fertilized and the offspring of each separately sown, with the result that, whereas from recessives he obtained only recessives in any number of succeeding generations, the offspring of the dominants were not at all alike, in that they gave, first, pure dominants which, like the recessives, produced pure dominants indefinitely and second, cross-breds which while *appearing* dominant, nevertheless contained recessive characters and when self-fertilized produced once more dominants and recessives in the ratio of three to one. But of the apparent dominants one only was pure to every two which, although mixed, showed only the dominant trait. Therefore by

self-fertilization the original cross-breds produce out of every hundred:

25 D : 50 DR : 25 R

Like the pure R's, the pure D's are thenceforth pure.

The 50 DR's again have mixed offspring:

1 D : 2 DR : 1 R = apparently 3 D : 1 R

It was found that by working with combinations of two characters the results were the same although naturally more complicated.

Mendel's laws may be thus stated. When two parents that show contrasting characters, one dominant, the other recessive, are crossed, the offspring will resemble the dominant parent only in respect to the character in question. When these hybrid offspring are crossed with each other, the progeny will be mixed, 25 per cent resembling the dominant grandparent, 25 per cent the recessive grandparent, while the remaining 50 per cent will again be hybrid like the parents but will resemble the dominant grandparent. Thus 75 per cent will *appear* dominant and 25 per cent recessive, the ratio being on the average three to one.

There are three principles upon which these laws are based:

1. *Independence of unit characters,* traits being inherited as units.

2. *Dominance.* Unit characters are inherited through genes or determiners, and even when inherited the recessive characters cannot appear, if dominant characters also are present.

3. *Segregation* or purity of the germ cells. Each body cell of a hybrid contains genes for both of the contrasting characters, but during the process of maturation the chromosomes are halved, one gene for each character being discarded, so that but one remains, either dominant or recessive, as the case may be. Impregnation restores the number of chromosomes and genes but there is still only one gene from each parent for each character. Thus, if both genes are for the dominant character, the offspring will be pure dominant; if both are recessive the offspring will be pure recessive; if one is dominant, the other recessive, the offspring will be hybrid; but only the dominant character can be manifest in the body.

Castle, for example, has experimented with guinea-pigs with some interesting results, the contrasting characters being white or

black color, short or long hair, smooth or rough coat. In mating those of contrasting colors he finds that in the first generation all of the offspring appear black, which is the dominant color. When two of these are mated, their offspring, if four in number, will contain three black and one white individuals. The latter, mated with a white individual, will produce white forever. Of the black, but one is pure, the others having combined characters of which, however, only the dominant one is visible. The pure black mated with

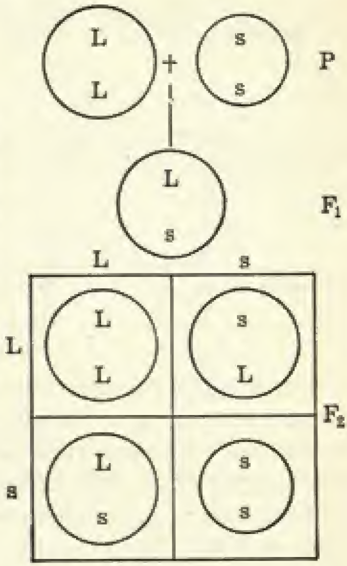
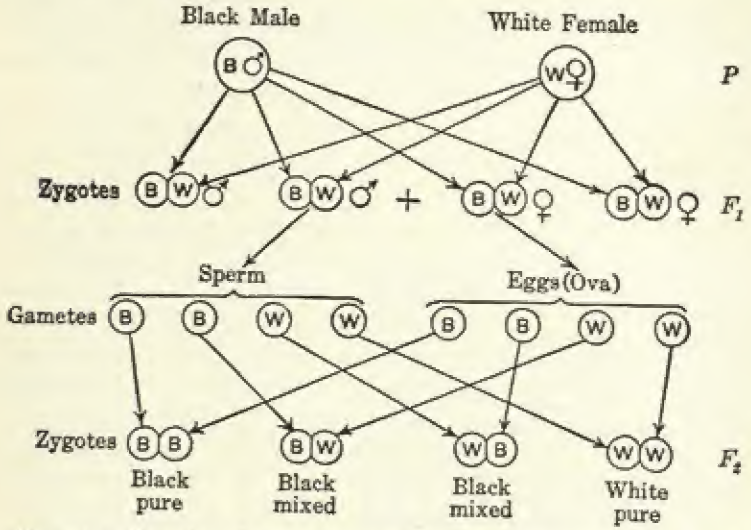


Fig. 15.—Results of crossing large size (L) and small (s) pea plants. The circles represent the zygotes and the character of the soma (phenotype), the letters within the circles the germinal constitution (genotype). The letters outside the recombination square represent the gametes. Each parent P represents a different phenotype and genotype, all the F_1 generation belong to the same phenotype and genotype, although but one is shown in the diagram, while in F_2 there are two phenotypes and three genotypes. Of the former there are three large (dominant) phenotypes to one small recessive. (After Woodruff.)

another pure black would have black offspring forever, while if the cross-breds were mated, their offspring would be in the ratio of three to one, and so on.

A further interesting experiment was the transplanting of the ovaries of a young *black* female into a white one. The latter was then bred to a white individual and whereas a normal white individual cannot have any black unit-characters in its germ cells and therefore should produce only white indefinitely when mated with another white one, the offspring of this union were black, showing conclusively that the inheritance lies in the germ cells, and that this somatic characteristic of the foster-mother in no way influenced the offspring, although all of its nourishment both *in utero* and later was derived from her body.

A diagram, which has been modified from Castle to illustrate the Mendelian law as applied to the single unit-characters of black B and white W, follows.



Occasionally the dominant contrasting characteristic of the parents is not exhibited in all of the cross-mated young in the same degree, but a blending of dominant and recessive traits may occur. Thus among silk-worms, a cross of the Shanghai variety, which has a white cocoon, and the Yellow Var with a rose-yellow one produces a form whose cocoons are straw-yellow. Again the blend may be a chemical one, as in grapevines, of which the Aramon coloring matter has the chemical formula $C_{46}H_{36}O_{20}$; the Teinturier has the formula $C_{44}H_{40}O_{20}$; and the Petit-Bouschet (hybrid) has the formula $C_{45}H_{38}O_{20}$.

With peas, Mendel bred one 1 foot high with another 6 feet high, producing an hybrid with a height varying from 6 to $7\frac{1}{2}$ feet; while the crossing of the flower *Mirabilis jalapa* female (red) with the male (white) produced offspring with red, white, and red-white streaked flowers, the last being an instance of mosaic inheritance. In many instances exhibiting at first blended inheritance, the regular three to one splitting of dominant and recessive characters may occur in subsequent generations.

Mendel's laws, therefore, are apparently a generalization of the greatest importance and apply universally to all cases of inheritance.

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CHAPTER VIII

ARTIFICIAL SELECTION

Under the general heading of selection are three aspects—Artificial, Natural, and Sexual; the first being, as the name implies, a man-made process which is interesting as indirect evidence of evolution, for the plasticity of animals and plants in the hands of the breeder shows that remarkable changes in the character of organisms can occur, and if produced by Man, why not by Nature, which is vastly more influential and has time without stint at her disposal?

The processes of artificial selection are undoubtedly more or less analagous to those of natural selection and aid us, as they aided Darwin, to understand more clearly the methods whereby Nature works to accomplish her results. It seems wise, therefore, to discuss this aspect of selection first as an introduction to the general theme.

Artificial selection is the process whereby the various breeds or races of domestic animals and plants have been formed by man. It is of the character of experimental biology upon which modern investigators rely so largely for their facts; but it has been found that laboratory experiments sometimes succeed where Nature fails, so that it is quite possible that the theory of natural selection, for instance, rests too largely upon an assumed analogy with the artificial.

Artificial selection is, in its simplest aspect, an extremely old process, judged by human standards, extending as it does over at least seven thousand years, and some of the changes wrought among animals and plants are truly marvellous. Certain types, on the other hand, like the peacock and guinea hen, lack plasticity and all the centuries of their domestication have failed to produce any very marked departure from the original stock. Such are static in contrast to the more plastic forms.

Nature of the Product.—The forms produced by artificial selection are often very far from a natural ideal and are not such as would be produced or even survive in the wild state. In nature,

characteristics which make for success in the struggle for existence are the product of evolution; in domestic races the qualities or traits which are useful to man or conform with his fancy or with style are selected, many of which would prove an insuperable handicap in open competition. Another characteristic of artificial breeds is their instability, their proneness to revert to the original type in a few generations if the vigilance of the breeder in prohibiting promiscuous mating between different varieties is relaxed.

Examples of Artificial Selection

Pigeons.—Among the most plastic of all domesticated animals are the pigeons, of which considerably more than 150 named varieties, all descended from a single known source and breeding, were known at the time of Darwin (1868); moreover, the range of variation is so great that some domestic races of the rock-pigeon differ fully as much from each other in external characters as do the most distinct natural genera (Darwin). (See Pl. I.)

The rock-pigeon, *Columba livia*, which includes two or three closely allied subspecies or geographical races, is to be regarded as the common parent form. From this conservative bird there have been derived some remarkable types, such, for instance, as the pouter, in which the body and legs are elongate and the feet are fully feathered; but the most peculiar feature, which gives the name to the variety, is the enormous size of the œsophagus, which is often inflated, giving the bird a remarkably pompous air. A second variety consists of the carrier pigeons, with elongated beak, neck and body but with the eyes surrounded by much naked, generally wattled skin. These pigeons are capable of the most sustained flight and are used abundantly as homing birds. They gave remarkable service as messengers during the World Wars.

In the fantail variety, the tail is expanded, directed upward and formed of many feathers, with no oil gland, and there is a rather short body and beak. The carriage of this bird is remarkable, the head touches the tail feathers, and habitually trembles very much, and the neck has an extraordinary backward and forward movement. Good birds walk in a singular manner as if their feet were stiff, and owing to their large tails they fly badly on a windy day.

The turbits have the feathers reversed along the front of the neck and breast while in the Jacobins they are reversed even more

along the back of the neck, forming a hood which, meeting in front of the neck, almost encloses the head. Tumblers have a curious habit of tumbling backward during flight, some, particularly the Dutch Rollers, tumbling to an extraordinary degree. "Every few seconds over they go; one, two, or three summersaults at a time. Here and there a bird gives a very quick and rapid spin, revolving like a wheel, though they sometimes lose their balance, and make a rather ungraceful fall, in which they occasionally hurt themselves by striking some object" (Brent in Darwin).

In the Indian frill-back, as in the Jacobin, the feathers are reversed, but in the frill-back they curl backward over the whole body. The trumpeters have a tuft of feathers at the base of the beak curling forward, and a very peculiar voice.

These instances, the descriptions of which have been taken from Darwin, will suffice to show not only the extremes of variation but the impossibility of natural survival on the part of some of them, notably the tumblers and fantails, with their poor locomotive powers, and the frill-backs, whose feathers, instead of being an admirable protection against inclement weather, actually invite the destruction of the bird. The young of all of the highly improved fancy birds are extremely liable to disease and death owing to the detrimental effect produced on the constitution of an animal by too close inbreeding. Some of these breeds are very old, pouters, Jacobins and tumblers having existed prior to 1600. Nevertheless they are not yet stable and it is said that only two generations of promiscuous breeding will suffice to produce a mongrel in many ways an apparent reversion to the ancestral rock-dove type.

Factors of Artificial Selection

The means employed by the stock breeder in the production of new varieties have been enumerated by Jordan and Kellogg as follows:

First, **unconscious selection** with more or less complete isolation. What this really means is a weeding out of the unfit, a sort of lethal selection of the less desirable animals from every point of view. These are eliminated and the remaining animals permitted to breed. This improves the stock without giving the race distinctive qualities. Nevertheless where isolation is effective and environmental conditions differ, it leads in time to marked racial

divergence. Among the sheep of England several markedly distinct breeds have been thus produced, as follows:

Hornless Varieties:

Southdown sheep of Sussex, tawny face and legs.

Hampshire sheep, black face, ears, and legs, black spot under tail.

Devonshire sheep, similar to preceding but without black spot under tail.

Cheviot sheep, face and ears white, head free from wool, ears erect.

Shropshire sheep, dun face, face more or less covered by wool.

Horned Varieties:

Dorset sheep, white face and ears, small white curved horns.

Irish sheep, black horns.

Second, **conscious selection of the more desirable individuals,** (methodical selection) emphasizing such points as larger size, plumpness, earlier maturity, greater docility, and fertility. While unconscious selection tends to produce racial divergence, here the reverse is true, for these good qualities appearing in all individuals tend to obscure natural or racial traits and make all sheep look alike.

Third, **conscious selection directed toward definite or special ends,** that is, emphasizing certain individual characteristics rather than working toward a good, all-round animal. Variation is continually bringing new points to the breeder's notice; those which strike his fancy or increase the value of the animal will be cumulatively emphasized in successive generations by breeding only from those individuals which show the characteristic best. In this way increased milk-flow or yield of meat or wool, or the disappearance of horns is obtained. Often the character which strikes the breeder's fancy is non-beneficial and hence opposed to a result which would be produced by natural selection.

Fourth, **crossing or hybridizing.** The crossing of two individuals is often of great benefit because it (1) increases the range of variation, (2) adds or combines certain desirable characters, (3) eliminates the undesirable. The offspring of such crossing may vary greatly, especially after the first generation, and the qualities they show may be either good or poor. They will diverge widely from either parent or show a combination of the characteristics of

both. Sometimes traits appear that are distantly ancestral and again those that are entirely new. When this cross-breeding is accompanied by careful selection directed toward definite or special ends, remarkable results are accomplished, and it is mainly upon this series of processes that breeding as a fine art depends. In this way Luther Burbank has produced a marvellous assemblage of plant varieties, flowers, and fruits, attaining by his patience and skill results which are almost like those of wizardry.

Limits of Artificial Selection

These are not met with as soon among plants as among animals, and the first impediment is lack of fertility in making wide crosses. Among animals, crosses of varieties only are practicable and as a rule related species such as the horse (*Equus caballus*) and the ass (*Equus asinus*) can be bred only for one generation, as the offspring is almost invariably sterile. Among plants, on the other hand, not only are wider crosses practicable but many plants can be propagated from cuttings, while higher animals, including all domestic animals, cannot, and the only way of getting another individual such as a mule is to make the original cross again. Mules can be improved therefore only by improving the parents or by crossing different breeds of the horse and ass respectively.

Cross-breeding Contrasts.—Contrasting results are sometimes obtained in cross-breeding by reversing the sexes of the two varieties mated. Thus the common mule is the offspring of a male ass and female horse; from the father he inherits certain superficial traits such as the small hoofs, somewhat scantier mane and tail, voice, and some peculiar mental characteristics; while from the mother come the deeper-lying size and strength and symmetry. Some authorities claim that his intelligence is greater than that of either parent, although he lacks the dignity and poise of a good horse. Reverse the cross and the result is a hinny, more horselike in contour and appearance, but with the smaller stature of the ass. The voice is that of the horse, and the animal is more apt to be fertile than the mule. The superficial characteristics and voice are in each instance those of the father, the stature, strength and symmetry those of the mother (see Pl. II).

Among plants the reverse hybridizing of the walnuts gives another instance of contrasts. The California walnut (*Juglans californica*) male and the black walnut (*J. nigra*) female when pro-

pagated give trees which increase in size twice as fast as the combined growth of both parents, with clean-cut, glossy, bright green leaves from two to three feet long, an odor like apples, but no nuts. The hybrid is therefore sterile. From the male black walnut and the female California tree, however, there is produced a tree with larger nuts of a quality superior to that of either parent.

Mechanical Limits.—The second limit to artificial selection is a mechanical one, for just as architecture and especially bridge construction have their limitations fixed by the strength of the materials at the disposal of the builder, so a limit may be reached in nature. Speed among animals requires among other characteristics long and slender lower segments to the limbs, which reach their highest perfection in animals of the size of the average African antelope. With a larger creature, such as a horse, the impacts and strains to which the limbs are subjected are increased, not only because of the greater force required to move a larger animal, but very rapidly with each added increment of speed. The modern race horse with a speed of over thirty miles an hour has just about reached the limit of strength on the part of bone and muscle, and a marked increase on the part of future animals is not to be looked for without proportionate risk of frequent injury to the horse. There are known cases in which a positive limit has been reached in attempting to modify organs through selection alone.

Variations are nature's contribution to artificial selection and are the basis of all man's work, for he can create nothing, but must take the variations which nature provides, and there are definite limits to these variations.

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CHAPTER IX

NATURAL SELECTION

Natural selection still seems to be the most important factor in evolution and has been defined as "The survival of the most fit with the inheritance of those species-forming adaptations wherein fitness lies" (Jordan and Kellogg). Crampton says of it:

"Natural selection proves to be a continuous process of trial and error on a gigantic scale, for all of living matter is involved. Its elements are clear and real; indeed, they are so obvious when our attention is called to them that we wonder why their effects were not understood ages ago. These elements are (1) the universal occurrence of variation, (2) an excessive natural rate of multiplication, (3) the struggle for existence entailed by the foregoing, (4) the consequent elimination of the unfit and the survival of only those that are satisfactorily adapted, and (5) the inheritance of the mutations or recombinations that make for success in the struggle for existence. It is true that these elements are by no means the ultimate causes of evolution, but their complexity does not lessen their validity and efficiency as the immediate factors of the process."

Prodigality of Production.—Perhaps one of the most impressive things in nature is the teeming abundance of living creatures. The swarms of gnats dancing in the sunlight, the great number of birds on certain oceanic islands, the immense collection of individuals in a great school of fishes: all are examples of what Thomson has called the "insurgence of life," and when one realizes that he sees but the smallest fraction of the total numbers which occur, he is the more impressed. Speaking of the splendor of oceanic luminescence which is often met with at sea, Thomson says:

"There is a cascade of sparks at the prow, a stream of sparks all along the water level, a welter of sparks in the wake, and even where the waves break there is fire. So it goes on for miles and hours—a luminescence due to the rapid vital combustion of pinhead-like creatures (*Noctiluca* and others), so numerous that a bucketful contains more of them than there are people in London . . .

"On the night before the new or full moon in the middle or latter half of December there occurs the remarkable swarming of the Japanese Palolo worm. It invariably takes place about midnight just after floodtide. At 1 A.M., Akira Izuka relates, the worms 'covered the whole water as with a sheet' and were thick down to a depth of a fathom. By 2.15 A.M., there was not a single worm to be seen; the reproductive orgasm was over. The phenomenon appears to us to be a dramatic instance of the abundance of life, of the crisis-nature of reproduction, and of the precise way in which internal rhythms may be related to external periodicities."

The productivity of all living organisms is far beyond the ultimate numbers which can possibly survive, and the reason is this: organisms at their least rate of increase reproduce in geometric ratio, whereas the space they may occupy and the available food supply remain constant. Hence without some very efficient check the slowest breeders would soon exhaust the possibilities of food and space. For example, the elephant is the slowest breeder among mammals, but Darwin calculated that a single pair beginning to breed at thirty years and continuing to do so until a century old would produce on the average six young and would have in 750 years, barring accident, nineteen millions of descendants. A rabbit, on the other hand, may have six young in a litter and four litters in a year, and the young may begin to breed at six months, a vastly more rapid rate of increase than that of the elephant.

Among the lower vertebrates where no parental care is given to the young the potential productivity is necessarily enormous. In four herring the number of eggs varied from 20,000 to 47,000; in a cod there were 6,000,000; a turbot, 9,000,000; and a ling, 28,000,000, and yet despite the enormous number of offspring which might *possibly* be produced from a *single pair in one generation*, the ultimate number of herring or cod or ling remains on the average about the same. The chance of survival, therefore, of a ling's egg is one in fourteen million.

The vertebrates, however, are relatively slow breeders, for there are as a rule but one or at most a half a dozen generations in a year. With invertebrates, on the other hand, the actual number of generations may greatly exceed this, and this is what Linnæus meant when he said: "Tres muscæ consumunt cadaver equi, æque cito ac leo." Huxley estimated that the descendants of a single green fly, if all survived and multiplied, would at the end of one summer

weigh down the population of China. Common house-flies would in the same time—six generations of three weeks each—occupy a space of about a quarter of a million cubic feet, allowing 200,000 to a cubic foot. An oyster may have 60,000,000 eggs, and the average American yield is 16,000,000. If all the progeny of one oyster survived and multiplied and so on until there were great-great-grandchildren, these would number 66,000,000,000,000,000,000,000,000,000,000,000, and the heap of shells would be eight times the size of the earth!

Professor Woodruff in his experimental study of *Paramecium* has maintained a pedigreed race since 1907, the descendants of one wild individual. In five years there were 3029 generations, the mean rate of reproduction being three divisions in 48 hours. They were as healthy at the end as at the beginning of the culture and had given evidence of the potentiality of producing a volume of protoplasm approximately equal to ten thousand times the volume of the earth! It has been estimated that at the end of the 9000th generation, now long since passed, the mass would exceed the confines of the known universe and the rate of growth would be extending its circumference into space with the velocity of light!

With such extraordinary productivity on the part of all living matter, the efficiency of the check upon every species of plant or animal is at once apparent. This check is that which Darwin and Wallace both recognized, and called the *struggle for existence.*

Struggle for Existence.—This struggle for existence is the competition between all organisms and between each individual and the physical environment. The struggle is threefold, although in the long run it is all against what may be called the environmental complex, which includes all surrounding nature, whether due to physical conditions, to plant or to animal life.

The *intraspecific struggle* is the struggle against the organism's own kind, the internecine strife. In some cases this is the most severe check of all, for each one's needs are precisely similar and the competition, instead of touching at one or two points, is absolute. In human warfare, the hatred is more bitter the nearer the contestants are related, as shown by Germany's "Gott strafe England!"; so it is with the organic world.

Examples of this intraspecific struggle are the young trees in a forest. As seedlings they may spring up over a devastated area

in great abundance. Some soon die from lack of sufficient soil or moisture or due to other causes, but they are still numerous until they become so tall that their branches begin to mingle and a leafy canopy is formed which shuts out light and air from the trees of less vigorous growth. Then the weeding out of the less fit begins and the number of trees in the area rapidly diminishes until ultimately the relatively few great trees in a mature forest are the result.

In artificial lobster culture, experiments have shown that it is better to turn the newly hatched young at once into the sea rather than retain them within the limits of the aquarium for any length of time, for they are their own worst enemies and the results of what may be called cannibalistic selection are more destructive to the race than competition with the natural environment.

Interspecific struggle is the familiar struggle between members of different species, often in the nature of competition, but perhaps more frequently because the one may afford food for the other. Mankind is just as much concerned in this interspecific struggle as any other form of life, but in general it is the lower organism, be it plant or animal, which is worsted in the struggle and must make good its losses or perish. The following statement comes from the Indian Year Book for 1928 (nearly the yearly average):

"The total number of persons killed by wild animals in British India during 1925 amounted to 1,962, as against 2,587 in the previous year. Tigers were responsible for 974 deaths, leopards for 181, wolves for 265, bears for 82, elephants for 78, and hyenas for 6. Deaths were highest from tigers in Madras, from leopards in the Central Provinces and Berar, from wolves in the United Provinces, from bears in Bihar and Orissa and from elephants in Assam. Of the 376 deaths from 'other animals,' 73 were assigned to wild pigs and 98 to crocodiles and alligators. The highest number of deaths from all wild animals occurred in Madras (452), Bihar and Orissa, the United Provinces and the Central Provinces and Berar coming next in order. The mortality from elephants showed a marked increase in provinces where these animals are found wild. There has been a noticeable decrease in deaths from all other animals except bears in almost all provinces.

"Deaths from snake bite fell from 19,867 to 19,258. Decreases occurred in Madras, the United Provinces, the Punjab, Burma, Bihar and Orissa, the Central Provinces and Berar and Assam; but Bombay and Bengal have reported slight increases.

"During the year 21,605 wild animals were reported to have been destroyed, of which 1,609 were tigers, 4,660 leopards, 2,485 bears and 2,361 wolves. A sum of Rs. 1,55,667 was paid in rewards, against Rs.

1,69,765 in the previous year. The number of snakes destroyed in India proper decreased from 47,106, to 41,004, and the rewards paid for their destruction were Rs. 1,579 as against Rs. 1,403 in the previous year."

Instances could be multiplied *ad libitum*, as the struggle is universal and no creature is immune, although in more favored communities, with rare exceptions, only parasites and disease germs make their direct attack upon man, but *every animate form* depends upon some other organism, be it animal or plant, for its food, so none is exempt from direct or indirect participation in the universal strife.

Environmental struggle is that against the physical environment —against excess of moisture or of drought, against extreme heat or cold, against lightning and tempest, earthquake and volcanic eruption. The eruption of Mont Pelée in May, 1902, slew practically every inhabitant of the city of St. Pierre, there being but one lone survivor out of a population of perhaps 28,000 souls; while in August, 1883, the volcano of Krakatoa as the culmination of a series of increasingly violent explosions threw back the inpouring sea and drove a wave of water high upon the neighboring coasts of Java and Sumatra, engulfing more than 36,000 people with their villages and lands (Iddings). The Sicilian earthquake of December 28, 1908, caused the death of at least 77,283 people in Messina and the near-by city of Reggio, while the official figures for the Japanese earthquake of 1923 are: killed 103,000, injured 125,000, missing 235,000, a total of 463,000 souls! Again, as a result of neither earthquake nor volcano, the great tropical storm of September, 1900, piled up the waters of the Gulf of Mexico, almost overwhelming the city of Galveston, with a loss of about 5,000 lives. The destruction wrought by our western cyclones and tornadoes is well known though rarely is there so appalling a loss of life as in the instances that have been given. Lightning is said to be the greatest single cause in the destruction of ranch cattle in Nebraska, due, however, in large part to the conductive power of the wire fences against which the animals drift before the storm. Thus the lightning bolt which would in a state of nature be local in its effect has its danger zone very largely increased through human interference. River floods such as those of China take their annual toll of thousands of human lives and doubtless of many animals as well. The Cenozoic sediments on our western plains, formerly supposed to be those of extensive lakes,

are now interpreted very largely as river flood-plain deposits. The fossil animals which they contain, and which must number many thousands, are largely the accumulations of flood victims of ancient days.

Drought is another potent cause of destruction, not only of plants but of animals as well, for the drying up of a waterhole is frequently the forerunner of tragedy. Excessive cold for which the animals are not prepared is another cause, as in the case of the numerous skeletons of guanacos, a wild species, allied to the domestic llama of South America, which have been observed in Patagonia. Of these Hatcher says: "During the winter storms these animals would be driven from the surrounding plains to seek shelter in the river valleys and there, beneath embankments or in clumps of bushes, would be found the remains of such as, through old age or disease, were unable to survive the rigors of the storm they had sought to escape."

All three aspects of the struggle are, strictly speaking, with the conditions of life, and as we shall see, the interrelations of various organisms with these conditions are generally very intricate, and over against the record of a vast host of all living beings nature writes a sentence comparable to the handwriting on the wall: "Thou art weighed in the balances, and art found wanting." But the destruction is not without distinction, for although the boldest and best of a race are sometimes the first to be destroyed, and often the slaughter is utterly indiscriminate like that in the trenches of Flanders, or when a great Greenland whale rushes through an immense school of the delicate sea-butterflies which form the bulk of its food, during which thousands are engulfed and swallowed, no perfection of detail nor harmonizing color nor activity nor any other usually advantageous variation availing one any more than the other; nevertheless, taking nature as a whole, the fittest do survive in the long run and the least fit are the first to perish.

Survival of the Fittest.—The survival of the fittest is therefore the result of natural selection. While the same conditions persist, specific change is very gradual, but with changing conditions placing a premium on new or different characters, species also undergo a change. Natural selection therefore enforces adaptation, and of two forms in competition, the adaptable will crowd out the inadaptable.

This is forcibly illustrated by the Tasmanian wolf or thylacine (*Thylacynus cynocephalus*) which is confined to-day entirely to the island of Tasmania but whose remains are found in the superficial deposits of the Australian mainland, showing it to be but recently extinct. The thylacine is one of the native pouched animals or marsupials (page 255) which form the indigenous mammalian population of Australasia and is characterized among other things by being dull of wit as compared with a true placental dog. Australia has such a dog, the dingo (*Canis dingo*), the origin of which is doubtful, but it is supposed to be of Asiatic extraction and introduced into Australia by human agency. We have here the adaptable placental placed in competition with the inadaptable marsupial, with the inevitable result—the marsupial holding its own when it had only the ancient enemies of its race to contend against, but powerless in competition with the representative of a more vigorous stock.

Nature's Balance.—Competition is inseparable from life and is really the source of all progress, but this very competition leads to a nicety of adjustment between rival organisms and a linking together of other beings into a marvellous web of interrelationships. This nicety of adjustment is known as nature's balance, and, although often unobserved, man has inadvertently sometimes upset the adjustment, causing dire results which he knows to his cost.

Not all organisms are enemies, as we have seen in discussing the biotic relationships of animals in Chapter II, but in many instances, although generally among unrelated forms, there is a marked interdependence, all of which adds to the complexity of the web of life, and at first sight the extremes of a series of interrelated organisms, when the links in the chain are unknown or disregarded, make them seem very far-fetched as illustrations of the case in point. Such, for example, is the linkage suggested by Darwin between domestic cats and red clover, but when all of the links are known, the connection is at once evident. Darwin found by experiments that humble-bees are almost indispensable to the fertilization of the heartsease (*Viola tricolor*), for other bees do not visit this flower. He also found that the visits of bees are necessary for the fertilization of some kinds of clover; "for instance, twenty heads of Dutch clover (*Trifolium repens*) yielded 2290 seeds, but twenty other heads protected from bees produced

not one. . . . Humble-bees alone visit red clover, as other bees cannot reach the nectar. . . . Hence we may infer as highly probable that, if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great measure on the number of field-mice, which destroy their combs and nests; and Col. Newman, who has long attended to the habits of humble-bees, believes that 'more than two-thirds of them are thus destroyed all over England.' Now the number of mice is largely dependent, as every one knows, on the number of cats; and Col. Newman says, 'Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.' Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of flowers in that district!" Huxley had added a link to each end of this chain of relationship by the supposition that the cats are very largely harbored by the unmarried spinsters on the one hand, whereas the clover affords sustenance for the cattle which in turn produce the "roast beef of Old England" which nourishes her valiant sons which are the source of England's might, thus making the number of maiden ladies in a community productive in this very roundabout way of the prowess of Great Britain.

It will readily be inferred from the foregoing how wonderfully delicate this balance of nature is in its adjustment and how easily it may be deranged by human interference. A few notable examples of such derangement of the balance may be given. The English sparrow was introduced into a city of Connecticut for the purpose of eradicating the measuring worms which were defoliating the elm trees at the time so characteristic of the town. It may be said to its credit that the sparrow did largely abate the nuisance for which it was imported, but owing to its fecundity, greediness, and quarrelsome disposition, it has become a widespread pest, driving out the native song and insectivorous birds and offering in exchange only its own unattractive personality.

Another instance is the Colorado potato beetle (*Doryphora decemlineata*), a native of the Central West, where it fed upon the nightshade and was kept in check by its natural enemies. The

introduction of the potato plant, a close ally of the nightshade, offered the beetle a new and abundant food-supply, to which it took with great avidity, multiplying rapidly, for the lessening of the competition for food rendered the other natural checks of relatively little avail. The beetles then began an eastward migration in an ever widening pathway, going from one potato plantation to the next, until they finally reached and extended along the Atlantic seaboard and now extract an annual toll equivalent to thousands of dollars from the raisers of the esculent tuber. In this case, it was not, as usual, the introduction of an animal into new environmental conditions that upset the balance, but the reduction of one of the most severe checks to survival, the struggle for food.

Another very remarkable instance the entire history of which is known is that of the gypsy moth (*Porthetria dispar*) which was accidentally liberated in Medford, Massachusetts, in 1869. Professor Léopold Trouvelot, a French naturalist, was experimenting with silk-spinning caterpillars, especially the American species, to see if any could be made of economic importance. He also imported specimens of the insect under discussion from Europe. Evidence seems to show that some of the egg clusters or young caterpillars escaped from his place, and as he was aware of the dangerous nature of the insect in its native home, he destroyed all the caterpillars he could find, but soon seeing that he could not fight them single-handed, he reported the matter to the authorities. Little notice was taken of the insects, however, although after a few years they did become exceedingly troublesome to the people of the neighborhood by defoliating their shade and fruit trees. During the summer of 1889, however, their depredations and numbers increased to such an extent as to become a public menace, depreciating the value of property and causing an exodus from the infested districts, as they swarmed everywhere and many trees and orchards died as a result of the repeated defoliation. The legislature of the commonwealth then took up the problem of extermination and appropriated the sum of $25,000 for their elimination. Additional appropriations were requested and granted until 1900, when the work of the state commission ceased. In the meantime another similar pest, the brown-tail moth (*Euproctis chrysorrhœa*) had also been introduced from Europe and, together with the gypsy moth, which spread alarmingly with the cessation of the work of extermination by the state, has become a problem of national impor-

tance. Hence the United States Government in coöperation with that of Massachusetts has taken up the fight. Actual extermination seems now out of the question, as every available method, mechanical, by poison, or by fire, has been tried, and what the authorities are striving to do is to restore nature's balance by introducing the parasites and other natural enemies of the two insects from their native home, with the hope that thereby they may be controlled and not become too great a burden, for their total destruction seems impossible.

Yet another noted instance is the introduction of the carnivorous mammal, the mongoose (*Herpestes griseus*), into Jamaica. "Rats brought by ships became a plague in Jamaica. To cope with them the mongoose was imported, and it made short work both of the Old World rats and the Jamaican cane-rats. But when these were gone, the appetite of the mongoose remained, and the poultry and various ground birds began to suffer. Useful insect-eating lizards were also eaten, and another cloud rose on the sky—there was a multiplication of injurious insects and ticks, so that plants and animals began to be affected through an ever-widening circle" (Thomson).

One instance where balance has been partially restored after being upset by human interference is in the case of a scale insect accidentally introduced into California from Australia on some young lemon-trees. This multiplied until it became a most pernicious pest which various mechanical remedies failed to control. Search was made in Australia, and a natural enemy, a lady-bug, was brought over to California, with the result that not only was the scale reduced but almost completely eliminated. It was then found that the lady-bug depended upon the scale for food to such an extent that it died in turn, and now protected colonies of scale and lady-bug are kept in readiness to control future outbreaks of the pest!

Survival of the Existing.—We have spoken of the survival of the fittest which controls the existence not only of a race, or the individuals which make up the race, but also of the characteristics which compose the individual. There are, however, certain characteristics which seem to be non-important and, so far as we can judge, have nothing to do with an organism's chance for survival. These non-essential characters are, as we say, not of selection value, and persist through heredity. They are minor traits such as pe-

culiar color patterns, relative proportions of parts, or vestigial structures, like the red color seen in the fins of certain deep-sea fishes. These forms live in a habitat where, as no light exists, the color can not be seen and hence is of no possible utility to the animal. The spots on the coat of a lion-cub are also instances in point. Usually these indifferent traits may be interpreted in the light of historic vestiges and point to former conditions in racial history where they were of importance in determining the chances for survival. To this category belong the great number of vestigial organs of which Wiedersheim has enumerated 180 in the human body alone! (See Chapter XXXIX.)

Summary.—The effect of natural selection as an evolutionary factor has thus been summarized:

1. Under new conditions harmful characters will be eliminated by selection.

2. Beneficial characters are intensified and modified.

3. The great body of characters neither hurtful nor beneficial will not be modified but will persist through heredity.

"The resultant of these existing conditions [of environment] is, according to Darwin and his followers, an inevitable natural selection of individuals and of species. Thousands must die where one or ten may live to maturity (*i. e.* to the time of producing young). Which ten of the thousand shall live depends on the slight but sufficient advantage possessed by ten individuals in the complex struggle for existence due to the fortuitous possession of fortunate congenital differences (variations). The nine hundred and ninety with unfortunate congenital variations are extinguished in the struggle and with them the opportunity for the perpetuation (by transmission to the offspring) of their particular variations. There are thus left ten to reproduce their advantageous variations. The offspring of the ten of course will vary in their turn, but will vary around the new and already proved advantageous parental condition: among the thousand, say, offspring of the original saved ten the same limitations of space and food will again work to the killing off before maturity of nine hundred and ninety, leaving the ten best equipped to reproduce. This repeated and intensive selection leads to a slow but steady and certain modification through the successive generations of the form and functions of the species; a modification always toward adaptation, toward fitness, toward a moulding of the body and its behavior to safe conformity with

external conditions. The exquisite adaptation of the parts and functions of the animal and plant as we see it every day to our infinite admiration and wonder has all come to exist through the purely mechanical, inevitable weeding out and selecting by nature (by the environmental determining of what may and what may not live) through uncounted generations in unreckonable time. This is Darwin's causo-mechanical theory to explain the transformation of species and the infinite variety of adaptive modification. A rigorous automatic natural selection is the essential idea in Darwinism, at least in Darwinism as it is held by the present-day followers of Darwin" (Kellogg).

Several objections to natural selection as a universal factor have been offered. Among them are the following:

1. It does not account for the beginnings of organs, which may appear at first as the veriest rudiments having as yet no selection value. As one has said, it accounts for the survival of the fittest, but not for the arrival of the fittest. Thus, to give rise to such specializations as elaborate mimicry, or the electric organ of the torpedo, etc., which are of apparent advantage only in the perfected state, natural selection, acting only upon minute gradations toward perfection, seems inadequate. The same is true of so complex a specialization as the eye and its function in the vertebrates or in the insects and crustaceans.

2. Over-specialization, of which there seem to be repeated instances such as the huge antlers of the extinct Irish deer which in some instances outweigh the entire skeleton, or the immense spiral tusks of the Jefferson mammoth, or the minute fidelity of certain mimicking insects such as *Kallima* (Fig. 30): all these point to the apparent impossibility of natural selection as an agent, for it is inconceivable that natural selection would exert an influence beyond the point of greatest usefulness to cause the organ to become a hindrance and not a help nor would it extend to fineness of detail in mimicry far beyond the most æsthetic perception of the enemy to appreciate. The objection to this objection is the absence of absolute proof that these are rightly interpreted as over-specializations.

3. Natural selection cannot account for degeneracy. To say an organ is no longer useful and hence disappears, is to state the effect and not the cause. If under changed conditions a character built up by natural selection becomes a menace, the reversal of

selection can accomplish its removal, but this will not suffice where the characteristic is an indifferent one. Thus it will be seen that whereas natural selection may be conceded to be a factor of importance, it is apparently not the only factor nor indeed the only important factor in the evolution of organic life.

There are those who object to natural selection because it is essentially a materialistic doctrine, depending as it does purely on the laws of chance.

"But this kind of formal summary of the tactics," says Thomson, "is quite fallacious. It conceals the heart of the matter, that living creatures with a will to live, with an insurgent self-assertiveness, with a spirit of adventure, with an endeavour after well-being—it is impossible to exaggerate the personal aspect of the facts, even if the words which we use in our ignorance may be too metaphorical—do trade with time and have commerce with circumstance, as genuine agents, sharing in their own evolution. There is abundant room for sympathetic admiration of the tactics of Animate Nature, though the strategy may—and for science, must—remain obscure."

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CHAPTER X

SEXUAL SELECTION

Sexual selection is the second Darwinian factor, the one whereby Darwin sought to account for the secondary sexual characters of animals, many of which seemingly cannot be the result of natural selection, for the modifications may not be useful in the struggle for existence.

Primary Sex Distinctions

The primary sex distinctions are the functional ones which naturally differ in the two sexes. They are the reproductive organs, ovaries and testes, with their essential glands and ducts, and the organs in the female whereby the young are nourished and developed before and after birth, the placenta and mammary glands.

Secondary Sex Characters

The secondary sex characters, on the other hand, are such as are often not directly concerned with procreation but may nevertheless be of considerable importance to the organism. They often enable us readily to distinguish the sexes, as in the case of the pea fowl (*Pavo cristatus*), whereas in other instances sexes may be only recognizable by a microscopic examination of the reproductive glands, as in the American oyster (*Ostrea virginica*).

Special Organs for Mating.—The secondary sex characters may be grouped under several headings for the purpose of discussion. First among them are special organs for mating, structures sometimes found in the male in addition to the normal devices for coition, which are primary sex organs. Such, for example, are the holding organs in the male frogs, curious pad-like structures on the thumb of the hand, by which the female is firmly clasped on either side of the hip girdle. Its purpose is to keep the two sexes together, as there is generally no internal impregnation but the eggs are fertilized in the water, which must be done immediately after extrusion before the gelatinous envelope has time to swell, since after that impregnation is impossible. The shark-like fishes, with one

living exception, have a portion of each pelvic fin in the male modified into what is known as the clasper for use as an intro-

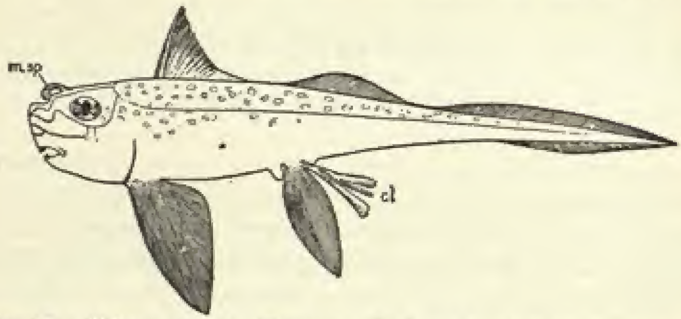

FIG. 16.—Chimæroid fish, *Chimæra colliei*, male, showing secondary sex characters. *cl*, claspers; *m. sp*, frontal spine (clasper). (Modified from Dean.)

mittent organ in mating, while in the related chimæroids or silver sharks there is in addition to the pelvic claspers a curious device on the top of the head, which looks not unlike a door-knocker and is provided with hooks derived from the skin. The actual use of this knocker-like organ has never been observed, but it is also supposed to be a clasping mechanism (see Fig. 16).

FIG. 17.—*Argonauta argo*, male. *hc*, hectocotylized arm. (After Claus-Sedgwick.) (For female see Fig. 111.)

The cephalopods show a remarkable seasonal alteration of one of the tentacle-like arms in the male which is used in mating, a modification known as hectocotylization (Gr. ἑκατόν, hundred, and κοτύλη, hollow vessel). The arm is filled with the spermatophores prior to coition and is detached from the male during the latter process, a new one being developed to take its place (see Fig. 17).

Brooding Organs. — Another kind of secondary sex characters are the brooding organs found especially in the female but sometimes in the male. Under this

head comes the pouch of the female marsupial mammal, either one transverse or two longitudinal folds of skin which cover the teats and serve to protect the very immature and helpless young until they are able to fend for themselves. A comparable device is seen in the sea-horse (*Hippocampus*, Fig. 18), a small but highly specialized fish in which the ventral fins have been modified into a brood pouch to carry the eggs until time for them to hatch. In this case, curiously enough, it is the male which, as Thomson says, "carries the eggs about in his breast-pocket." The same is true of some related pipe-fishes (*Syngnathus*).

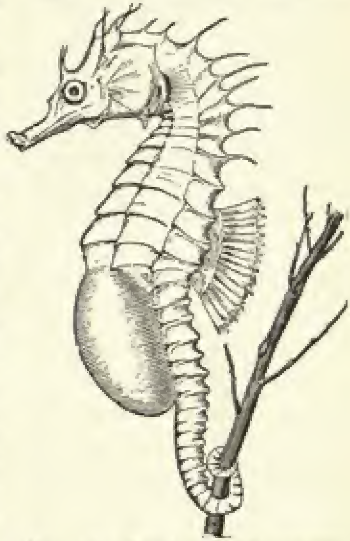

Fig. 18.—Sea-horse, *Hippocampus antiquorum*, male, showing brood-pouch formed from combined pelvic fins. (After Doflein.)

The frogs and toads also show marvellous brooding devices, especially the famous Surinam toad (*Pipa americana*) in which the skin of the back of the female forms growths for the reception of the eggs and in these the young undergo their whole metamorphosis. Each receptacle consists of a cavity with a lid; the origin of the latter is not understood but it is probably produced by the remnant of the egg-shell itself, which, after the larva is hatched, remains on the top of the cup. Gadow says of this group: "The greatest charm of the Anura [frogs and toads] lies in their marvellous adaptation to prevailing circumstances; and the nursing habits of some kinds read almost like fairy-tales."

Special Sense and Sound-producing Organs.—A third instance of secondary sex characters is represented by special sense and sound-producing organs. Here it is the insects which form the best means of illustration, for being as a rule active locomotor types, their special senses are proportionately developed. Male moths, especially the so-called giant silk-worm moths, the cecropia, polyphemus, luna, and others, have the feathery antennæ enormously developed compared with those of the female. They are the seat of a remarkable sense which, for want of a better under-

standing has been compared with the human sense of smell. It is used by the male in searching out the female for the purpose of mating, and is wonderfully effective, the male moths assembling around a newly emerged female from a radius of several miles. Among the scale insects (coccids, Fig. 19) both sexes are degenerate sedentary types during their young condition and often obscurely colored so as to be discerned with difficulty. The female remains scale-like throughout life but the male upon metamorphosis changes into a delicate two-winged fly in sharp contrast to his lowly mate. Abortion of the mouth parts in adult insects is not infrequent, as in the Chinese silk-worm (*Bombyx mori*), may-flies, etc., but in the male coccid they are replaced by an extra pair of eyes on the under side of the head as a necessary aid in finding the obscure female!

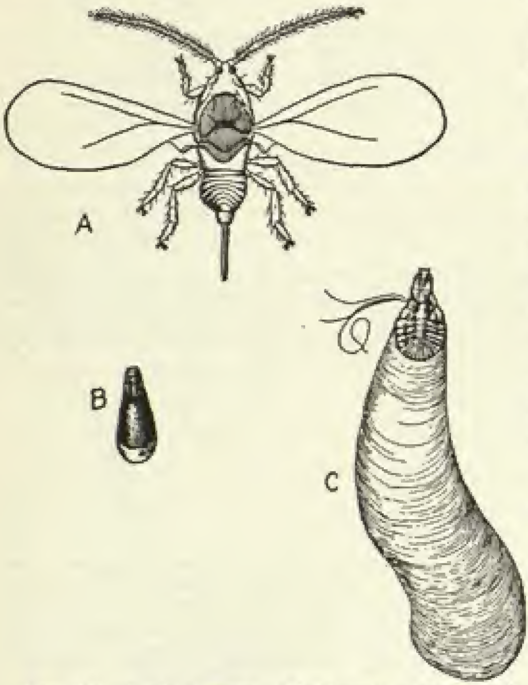

Fig. 19.—Scale insects, *Mytilaspis pomorum*. A, adult male; B, young male scale; C, adult female scale and egg capsule. Greatly enlarged. (From J. B. Smith's *Economic Entomology*.)

Vocal organs are almost exclusively confined to the vertebrates, with the exception of the insects, but in the latter the males only are provided with sound-producing organs. With the crickets and katydids they are a modification of the fore wings, which have sonorous structures that are thrown into vibration by being rubbed past each other, the sound being amplified by tightly stretched membranes analogous to a banjo head, or by resonant chambers formed by the wings, and comparable to the body of a violin.

The grasshoppers rub the hind leg across the edge of the wing, and the cicadas have a remarkable pair of kettle-drums at the base of the abdomen which are made to resound by the alternate stretching and relaxing of the membrane which covers them. They lie beneath a pair of backwardly projecting flaps comparable to the skirts of an eighteenth-century waistcoat.

Special locomotor organs, such as occur in the male scale insects and certain moths, are perhaps not so much a development in the male as degeneracy in the female, for absence of locomotive powers on her part renders increased activity upon that of the male imperative for the sake of future generations. In the famous gypsy moth, the female, although still possessing wings, has lost the power of flight because of the great weight of her body, while in the canker-worm moths the female's wings have utterly disappeared.

Organs of special use usually take the form of weapons such as the antlers of the male deer, the tusks of the boar and of the male musk deer and chevrotains, and among insects the huge mandibles of the stag-beetles and the spines on the head and thorax of the rhinoceros-beetles. Among bees and wasps, on the other hand, the sting is confined to the females or to the so-called neuters or workers which are in reality undeveloped females. The sting is a modification of the ovipositor or egg-laying organ characteristic, for instance, of the parasitic Hymenoptera which are near relatives of their stinging allies.

Special characters for exciting or attracting the opposite sex are such as appeal to the senses of sight, hearing, and smelling, taking the nature of cries and antics, of color and plumage, and of special odors. They may be either seasonal or persistent and are in many ways the most inexplicable of all the secondary characters of sex. They are of course confined almost entirely to the male. Instances may be multiplied indefinitely, as they have been observed by all—the gorgeous tail of the peacock, the pompous dignity of his carriage and even his strident voice are all supposed to make an irresistible appeal to the female. The strutting of the common turkey and especially the drumming of the ruffed grouse are further instances. The beard of man and the mane of the lion may also be included under this head.

Reciprocal organs are found in a reduced state in the female, as horns in the goats, antelope, caribou, and reindeer. Stridulating organs, though undeveloped, are present in female crickets and

katydids, while in male mammals the mammæ are present in a rudimentary state. In the male, the mammary apparatus normally becomes absorbed, though occasionally at birth and at puberty milk is produced in the human subject. Male goats and castrated sheep have also been known to give milk (Wiedersheim). A functionless rudimentary brood pouch is present in the male Tasmanian wolf (*Thylacynus*).

Indifferent Characters.—Under the head of indifferent characters are included such as are of no vital importance to their owner and yet are sex distinctive. They are mainly the negative reciprocals of certain structures already mentioned as characteristic of the opposite sex, as for instance, the reduced wings of certain female insects, the vestigial gut in the male rotifers or wheel animalcules, the slight differences in size or color in many birds and insects, or the differences in the proportions or the pattern and arrangement of the veins of insect wings and in the number of tarsal or antennal segments.

Atavistic characters are those distinctive of ancestral conditions, like the hairy chest and greater bodily strength which often occur in men but rarely in women.

These are the secondary sex characters to explain which the theory of sexual selection was proposed, but it will be seen that with the exception of those under the caption of indifferent characters, and perhaps the last three, they *may* all be regarded as the result of natural selection, as they are useful in the struggle for existence. The characteristics included in the special characters for excitation, etc., on the other hand, are such as make their owner more conspicuous and doubtless expose him to dangers from which a more obscure animal would be immune. Hence their development is opposed to the principle of natural selection, as the results are a handicap and not an aid in the struggle for existence.

Theory of Sexual Selection

The theory of sexual selection is based upon the competition or struggle for mating, and while natural selection presupposes a passive female, sexual selection implies presumptive choice on her part of the most desirable male to be the father of her progeny, with the consequent inheritance by the offspring of his estimable characteristics. Darwin also included in his theory the competition or struggle for mating where rival males fight for the possession of

a female as in the case of the deer or the sea-lion, the female being in each instance the passive reward of the victor. But this fighting on the part of the males is merely a phase of the intra-specific struggle, although it is not a fight for food and space but for a chance to mate. This chance, however, often depends upon a life and death struggle and no theory of *sexual* selection is necessary to account for the development of the weapons or greater prowess which enables one animal to become the victor over another.

Postulated Bases of the Theory.—As Darwin originally proposed it, the theory was based upon the following assumptions, the truth of which was apparently attested by a varying number of facts:

"First, many secondary sexual characters are not explicable by natural selection; they are not useful in the struggle for life. Second, the males seek the females for the sake of pairing. Third, the males are more abundant than the females. Fourth, in many cases there is a struggle among the males for the possession of the females. Fifth, in many other cases the females choose, in general, those males specially distinguished by more brilliant colours, more conspicuous ornaments, or other attractive characters. Sixth, many males sing, or dance, or otherwise draw to themselves the attention of the females. Seventh, the secondary sexual characteristics are especially variable.

"Darwin believed that he had observed certain other conditions to exist which helped make the sexual selection theory probable, but the conditions noted are sufficient if they truly exist" (Kellogg).

Difficulties.—Some of the difficulties which stand in the way of our acceptance of Darwin's tenets are thus enumerated by Kellogg: The theory can apply only where the males are more numerous or polygamous, otherwise even if rejected by the first female each male, however undesirable, would sooner or later find his mate and thus the unornamented males would leave as many progeny as the ornamented, which would prevent any cumulation of ornamental variations by selection. Among the higher vertebrates, where a great number of ornamented males occur, the proportion of the sexes is about equal, and where polygamy exists there is always a struggle for mastery, not an active female choice.

In most species the mating female is observed to be wholly passive and propinquity is seen to be the greatest factor in determining which two shall pair.

Ornamental colors are as often characteristic of the males of species in which there is no real pairing as among those which pair. Sexual choice certainly cannot account for the remarkable ornamental colors of the males of many fishes in the breeding season, for the female may not even see the male which fertilizes her already laid eggs. Eigenmann, on the other hand, notes the utter absence of such ornamentation among cave fishes which live in the dark, and argues that where they do appear, therefore, they must be due to visual selection. This may, however, be explained in a different way, as we shall see (see page 141).

A high degree of the æsthetic sense on the part of the females of animals would be necessary for choice on a basis of ornament and attractiveness. For this we have no other proof, and we can not imagine its existence on the part of invertebrate animals in which ornament is often so highly conspicuous. Even among the higher forms wherein the æsthetic sense may be developed to a certain extent, we have no assurance of any one standard of beauty for individual taste varies greatly with men and probably also with animals. Even if we may attribute a certain æsthetic sense to mammals and birds, the question naturally arises whether it can be so keenly developed as to lead the female to make a choice among slight differences of color or song. Yet this assumption is necessary if the theory of sexual selection be accepted. Would not the evolution of this æsthetic sense upon the part of the female be just as difficult to account for? In all probability her reaction is purely emotional rather than discriminative.

Very few cases of actual choice by the female have ever been observed, for even so earnest an observer as Darwin himself, who had every reason to record the greatest possible number, failed to note more than eight cases among birds, and but half a dozen more, all doubtful, are mentioned in the literature from his day until 1907.

Many of the so-called attractive characters of males have been found to be during life of such a nature that the females could not note them; as, for instance, the brilliant colors and curious horns of the male dung-beetle which are so obscured by filth that they cannot be used for display, while in melodious or luminous insects like the crickets or fireflies, nearness will make a relatively feeble song or light seem much finer than that of a distant but much more musical or brilliant insect.

That dances and serenades do occur during the breeding season is well known, but they may be for the purpose of excitation of the usually passive female and may not imply the necessity of any discriminating choice upon her part among a number of males. That rivalry would be developed among the dancers or singers is only natural and may or may not lead to further perfection of the art.

Experimental Evidence.—There is as yet comparatively little evidence based upon actual experiment, but such as we have is strongly opposed to the sexual selection theory. In this connection the experiments of Mayer are of remarkable interest. He worked with the giant silk-worm moth *Callosamia promethea*, in which there is decided sexual distinction in color and pattern. The females have a reddish brown ground color, while the males are blackish, and the ornamentation in the two sexes is distinctly different. If there is any moth species in which the colors and general pattern of the male ought to be readily obvious to the female, and in which sexual selection might be presumed to have been the influence in producing a pronounced male type of preferred pattern, it is this species. The experiments were varied, but it was found that sight had nothing to do either with the finding of the female or choice of mate, for reversal of wings—male on female or female on male—or any other disguising of the sexes made no difference whatever in the mating. The assembling power, as we have already noted, was resident in the antennæ of the males.

From the experiments it is concluded that the mating instinct on the part of these two insects is a phenomenon of chemotaxis (Lat. *chemicus*, chemic, and Gr. τάξις, arrangement), as sexual selection on the ground of color alone does not affect it, and there is no associative memory connected with it.

Alternative Explanations.—It will be seen from the foregoing that the Darwinian factor of sexual selection rests upon very meager evidence, the great majority of secondary sex characters being explicable by natural selection, and on the other hand even where natural selection cannot be invoked, sexual selection does not stand the test of experiment. Some alternative explanation becoming necessary, the following have been offered:

"First, that the secondary sexual characters are produced as the result of the immediate stimulus (naturally different) of the sexually differing primary reproductive organs, this stimulus being usually considered to result from an internal secretion of the

genital organs acting on certain tissues of the organism; and second, that the males in most species possess an excess of energy which manifests itself in extra-growths, extra-development of pigment, plumage, etc., and that displays by the males of special movements, sound-makings, etc., are direct effects or manifestations of sexual excitation" (Kellogg).

In explanation of the first of these alternative theories it should be remembered that there are within the body numerous glands, some of which, like the salivary glands, liver or pancreas, have ducts connected with them, and these ducts bear away a definite secretion which, like the saliva, pancreatic juice, and bile, has a particular and well known function. In addition there is the group of so-called ductless or endocrine glands, such as the spleen, the thymus and thyroid bodies, and the suprarenal capsules. These are sometimes of considerable size and very constant in a large number of vertebrated animals; hence their importance is manifest, but is not in every instance clearly understood. They seem, however, to have a very vital regulating function of one sort or another and their serious derangement is always followed by or concomitant with disease. The reproductive glands, especially those of the male, are often large, seemingly unnecessarily so if procreation is their only function. Ductless glands known as interstitial have been demonstrated in connection with the testes or ovaries as the case may be, so that, in addition to the "normal secretion" of sperms and ova, there is poured into the blood stream an "internal secretion" consisting of the chemical messengers or hormones, which are known to control or stimulate the development of certain secondary sex characters, such as antlers, mane, or beard. Castration which removes the sex glands prevents the appearance of these characters; on the other hand, the injection of male hormones into a castrated animal restores its secondary sex deficiencies.

Steinach's experiments in which he reversed the reproductive organs in the two sexes of guinea pigs gave rise to amazing results, as the male then developed female traits, both physical and physiological, and vice versa, although they were unable to produce young. (Parker).

The excess of vigor in the male is due to the vastly greater task which the female has of providing nourishment for the offspring, either in the form of yolk in bird or reptile, or of interuterine nour-

ishment and milk in the mammal. With approximately equal vitality to begin with, the drain upon the female would lead to relative excess of energy on the part of the male which could manifest itself in the development of the male characteristics. As we shall see in a later chapter (Chapter XXIII), cave animals are characterized by depauperation, lessening of stature due to starvation. Excess of energy is inconceivable on the part of a cave salamander or fish and therefore could not give rise to exuberant growths. This may answer Eigenmann's argument (see page 138), at least in part. In order that the duty of procreation may not be shirked, it is necessary for the male to have increased activity and sexual instinct in proportion as the female is passive, which would account for the greater sexual excitation on his part.

A final explanation for secondary sex distinction is that of Emery, who believes that "many cases of secondary sexual differences are explained by the sudden appearance (mutation) of another form of male or female, the persistence for a while of the two forms side by side, as now exists in numerous dimorphic species (especially among insects), and then the gradual dying out (killing out by natural selection) of one of the two old original forms (the one like the other sex), thus leaving the other, or aberrant form" (Kellogg). This explanation is also offered to account for the development of mimicry among butterflies and will be further discussed under that head (see page 213). Kellogg seems to think that as an explanation for the development of sex characteristics it is rather far-fetched, but in the promethea moth which we have discussed the larger and more brilliantly colored individual is the female, which makes it difficult to apply the excess of male vigor theory, to say the least.

Morgan in his *Evolution and Adaptation* enumerates no fewer than twenty objections to the theory of sexual selection. He says by way of summary:

"Darwin's theory served to draw attention to a large number of the most interesting differences between the sexes, and, even if it prove to be a fiction, it has done much good in bringing before us an array of important facts in regard to the differences in secondary sexual characters."

Morgan does not think it has done more than this for the theory meets with fatal objections at every turn.

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CHAPTER XI

INHERITANCE OF ACQUIRED MODIFICATIONS

Lamarck's Laws.—Buffon, Erasmus Darwin, and Lamarck, as we saw in the first chapter, all developed evolutionary theories which had one thing in common, the inheritance by offspring of the modifications impressed upon the parent during its lifetime. Buffon believed that these modifications were the result of the direct action of environmental influences; Erasmus Darwin that they sprang from within through the reaction of the organism to outside conditions, applying his theory to both animals and plants; while Lamarck's belief was a compromise, setting forth views comparable to those of Erasmus Darwin as applied to animals and of Buffon with reference to plants. Lamarck's theory of evolution may be stated as follows:

1. The internal forces of life tend to increase the size of an organism, not only as a whole, but in every part as well.

2. Each organ or part is the outcome of a new movement which in turn is initiated by a new and continuous need or want.

3. The development of an organ is in direct proportion to its employment. Continued use strengthens the organ little by little until its full development is attained, while disuse has the opposite effect, the organ diminishing until it finally disappears.

4. All that has been acquired by an individual organism during its lifetime is transmitted by heredity to its offspring.

Neo-Lamarckian School.—Lamarck's second and third laws especially have a great deal of truth in them, but the crucial point in their acceptance as evolutionary factors is the truth or falsity of his last premise and herein lies the apparent impediment to the acceptance of his teaching, for the whole fabric of his theory depends upon it, and as we have seen, the Weismann law of heredity seems to controvert it beyond question. Nevertheless there has sprung up a group of writers who are in a measure the followers of Lamarck and to whom the name Neo-Lamarckian, as opposed to the Neo-Darwinian school (followers of Charles Darwin, championed by Weismann), has been given. Among the adherents

to the former may be found many pathologists (students of morbid anatomy), whose researches show the wonderful plasticity of the individual body, and the paleontologists, who see continually before them evidences of adaptation which seem to imply the action of mechanical forces (kinetogenesis) in their production, but few if any pathologists or paleontologists now believe in the inheritance of acquired characters.

Among the better-known followers of this school may be mentioned Herbert Spencer, the German savants Eimer and Haeckel, the botanist Naegeli, the American paleontologists Cope, Hyatt, and Dall, the zoölogist Packard, and the student of recent vertebrates Gadow, many of whom, however, did their work before Weismann's objection was published. What the effect of the latter upon their beliefs would have been, one can not say, but it would doubtless have been weighed very heavily by most of them. Weismann's theory of heredity admitted the possibility of the inheritance of acquired modifications among the Protozoa, lower Metazoa and lower plants, but not among the higher plants and animals; as Osborn (1891) says, however, it is difficult to see why so valuable an asset as the ability to inherit such characteristics and thus to profit by the failures and successes of past generations should ever have been lost through natural selection.

Weismann later admitted, and the view has wide acceptance, that the germ-plasm might become modified to a limited extent by certain environmental conditions, but that such modifications led to general and unpredictable changes in future generations which might be entirely different from those somatic changes in the parents which were directly produced by such environment.

Acquired Modifications

Acquired modifications are of such interest that it is well to enumerate the various sorts in some detail.

Restriction of Size.—Food supply profoundly affects the ultimate growth of an animal. A number of house-flies of the same species will be seen to differ materially in size around a certain average. This does not mean that the smaller ones are younger than the larger, for an adult insect when once it has attained the power of flight has ceased to grow. What it does mean is that the small fly, unless it belong to a different variety, was unable to secure sufficient food during its period of larval life, resulting in a

permanent dwarfing of the individual. Nothing is recorded, however, of any permanent effect of such dwarfing upon the race, while silk-worms, if meagerly fed for one generation, fail to attain the full optimum of size as adults for three generations, even though the larvæ are amply fed. With the succeeding generations, however, the moths become larger and soon attain their normal size. These temporary dwarfings are called inductions.

Permanent dwarfing is known to occur, as in the case of the dogs owned by the Indians around the Hudson Bay trading posts, which have been in their possession about forty years and are now much smaller than better fed dogs belonging to the same original stock, but owned by the white men of the posts. Other instances of permanent dwarfing are seen in the Shetland ponies, of which the average height is about 10 hands, though many do not exceed 9 hands. Whence the ancestral stock of these ponies reached the Shetlands is unknown, some writers suggesting a Scandinavian, others a Scottish origin, but some of them are cart-horse-like in build, others more slender and Arab-like. Whatever their origin, they are unquestionably derived from a much larger stock, and the diminution of size is apparently a direct response to circumscribed surroundings together with hard conditions and meager fare.

In the islands of Malta and Cyprus have been found dwarf races of elephants, the adult individuals ranging in height from three to seven feet, relics of the old armies of migration when these Mediterranean islands were part of a broad highway of communication between Africa and Europe. And here again the same causes which have dwarfed the Shetland ponies seem to have had their influence, for the small size and innumerable variations of these elephants are ascribed to the struggle for existence that such a reduced and unfavorable feeding ground would entail. These dwarf elephants are now entirely extinct, but seem to have been of the same stock as the African elephants of to-day, which in the fullness of their growth possess a stature second to no living terrestrial form.

The effect of these restrictions of food is in the nature of transmission of the maternal condition rather than true heredity, and doubtless for many generations the dwarfing was simply the result of ontogenetic repetition and meant nothing more; ultimately, however, the repeated starving seems to have made itself felt in hered-

ity, with the result of a permanently dwarfed race (see, however, page 145).

Mutilations have been one of the principal lines of research of those who would prove the inheritance or non-inheritance of acquired characters. Even when practiced for many generations or even for thousands of years (circumcision in man) these apparently fail to influence the unmutilated progeny in the slightest degree. Weismann, for instance, experimented on white mice, producing no fewer than 901 young from five successive generations of artificially mutilated parents, and yet there was not a single example of a vestigial tail or any other abnormality in this organ.

Hence we may safely say that variations due to mutilation and to disease are not inherited, otherwise in all probability none of us would exist without some trace of hereditary crippling. Of the effect of climate, on the other hand, we are not so sure, for many of the observed changes which an animal undergoes as a result of the influence of cold or heat or humidity or dryness may be of an ontogenetic nature.

Effects of Cave-Dwelling.—The strange modifications of cave-dwelling animals, which will be discussed in detail in Chapter XXIII, are the direct result, first, of lack of light in the loss of pigment and of organs of vision, and, second, of scarcity of food which gives rise to depauperated bodies and attenuated limbs. Certain organs, such as tactile or gustatory structures, have hypertrophied as those of sight have diminished, and while natural selection may be invoked to account for these well-developed structures, it cannot account for the atrophy of the others nor for the depauperation. Panmixia (see page 103) might *permit* these changes, but is of questionable value as a *cause*. Both of the principal American students of cave faunas, Packard and Eigenmann, feel the necessity of some other factor than the Darwinian, and Packard has expressed himself as follows with regard to the causes of production of cave faunæ:

1. "Change in environment from light, even partial, to twilight or total darkness, and involving diminution of food, and compensation for the loss of certain organs by the hypertrophy of others.

2. "Disuse of certain organs.

3. "Adaptation, enabling the more plastic forms to survive and perpetuate their stock.

4. "Isolation, preventing intercrossing with out-of-door forms, thus insuring the permanency of the new varieties, species, or genera.

5. "Heredity, operating to secure for the future the permanence of the newly originated forms as long as the physical conditions remain the same.

"Natural selection, perhaps, expresses the total result of the working of these five factors, rather than being an efficient cause in itself; or at least constitutes the last term in a series of causes. Hence Lamarckianism in a modern form, or, as we have termed it, Neo-Lamarckianism, seems to us to be nearer the truth than Darwinism proper or natural selection."

Inheritance of Instinct.—Instinct has been defined as "the natural unreasoning impulse by which an animal is guided to the performance of any action, without thought of improvement in the method" (Webster). It usually implies an action based upon inherited knowledge, but, judging from experimentation upon living animals, that knowledge is the result of trial and error upon the part of individuals which ultimately becomes part of the heritage of the race.

Birds are particularly interesting in this regard, for they possess so many instinctive traits, not only of food-getting and defense, but nest-building, migration, learning to fly in the mode characteristic of the species, and song. Many of these things have been attributed to actual instruction on the part of the parents or, in the case of the nest-building, to a recollection of the natal structure, but William Beebe tried the interesting experiment of raising a number of wild birds from incubated eggs. These, while never having had parental care or example, nevertheless manifested in each instance all of the instinctive actions of their race, although, as Beebe says, they were in some cases slower than they should have been about learning to fly, the maternal insistence being an aid in overcoming a very natural timidity on the part of the fledgelings.

So many of the curious manners and customs of domestic dogs, such as turning around three times to stamp out a lair, are doubtless relics of formerly valuable instinct, of little present worth to the house-dwelling associate of mankind, but perpetuated by heredity.

Ontogenetic Variations.—It is often a matter of great difficulty to determine whether characteristics shown by an animal are those

of the race (phylogenetic) or those of the individual (ontogenetic), even though observed in a number of successive generations where the life conditions remain the same. An interesting example is the brine-shrimp (*Artemia salina*) which has a wide-spread distribution from Great Salt Lake, Utah, to Central Asia. This creature is remarkable in several ways, as it can live in a 27 per cent brine solution on the one hand or in fresh water on the other. In some places the colonies seem to be altogether female, and parthenogenesis is the rule, the eggs developing without being fertilized. In other localities males are common and reproduction is biparental. Sometimes the brine-shrimp is viviparous, the eggs hatching within the brood-sac of the mother, and again it is variable in its form, especially as regards the end-lobes of the tail and the bristles they bear: all of which features seem to be correlated with the chemical diversity of the various habitats within which it is found (Thomson). The eggs can survive being dried and may be blown about by the wind or carried by the feet of birds

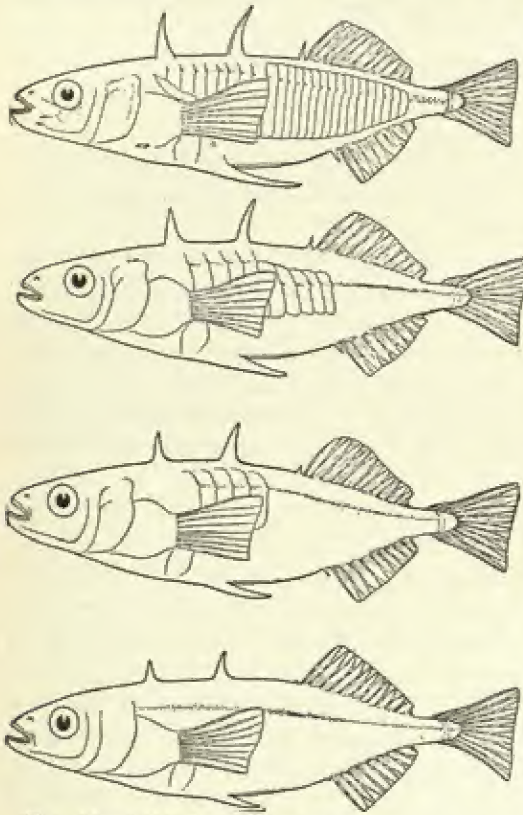

FIG. 20.—Stickleback fishes, *Gasterosteus cataphractus*, showing ontogenetic variation of plates and spines as a response to varying salt content of the water. Uppermost figure collected in salt water, the next in brackish water, the third at a river mouth, and the fourth in fresh water. (From Jordan and Kellogg's *Evolution and Animal Life*. [D. Appleton and Co.])

from one salt pond to another. They have also been bred from an English commercial product known as "Tidman's Sea Salt," of which a solution was allowed to stand for several days. A fresh-water ally, *Branchipus*, is said to be merely another phase of *Artemia*, the distinctions, as in most of the peculiarities of the latter genus which have been described, being largely due to the degree of salinity of the medium. If this be true, most of these variations are ontogenetic, as the transference of eggs to other conditions than those under which the parents lived would at once give rise to a variant from the parental type.

Experiments by Loeb upon the unfertilized eggs of sea-urchins have shown that artificial parthenogenesis can be caused to occur by chemical stimulus, either by adding or suppressing certain salts in normal sea-water, which is suggestive of the parthenogenetic conditions of certain colonies of *Artemia* mentioned above. Owing to the brine-shrimps' method of dispersal and the fact that salt ponds are often isolated and of various degrees of salinity, the change of habitat is apt to be an abrupt one which renders individual adaptability a highly necessary asset.

The little fishes known as sticklebacks (*Gasterosteus cataphractus*, Fig. 20), which have such curious nest-building habits, also show an ontogenetic variation dependent upon the chemical content of the water. Those living in salt water have from twenty to thirty bony plates along the back, in brackish water these are reduced to from fifteen to three, while in fresh water there are none at all.

As we have seen, it is often difficult to say whether the adaptive characters which are so often taken as criteria of species are racial or individual; if the latter, even though we may not know it, the form is an ontogenetic and not a genuine species, and it is highly probable that many of the observed instances of what was taken to be inheritance of acquired characters are not such in the true sense of the word but are simply due to the repetition of cause and effect in each individual generation. There is apparently an heredity control, however, for the adaptation to a change of habitat is not at random but always according to a definite plan, and gives rise to a predictable result.

Summary

To summarize what has been said: Lamarckism, even if true, would be incomplete in itself as an all-embracing cause of evolu-

tion, for while there are certain characters which it could well explain, there are others which it could not.

Lamarckism, therefore, is certainly not all-sufficient to account for the origin of new species, even if it were proved to be true; nor for that matter is natural selection. The latter seems, however, to be a factor of prime importance, as there is no impediment to prevent its impression upon the race as well as upon the individual. That acquired modifications influence more or less profoundly the development of every being is certainly true, and in many instances repetition of acquired effects, generation after generation, gives rise to *ontogenetic* species which may indeed simulate the phylogenetic. For these characters to become racial, however, implies an inheritance the means whereof we know not, in view of Weismann's brilliant but disquieting law of heredity. Until the universal application of this law shall have been refuted or a new mechanism of inheritance discovered, the Lamarckian factor as a means of evolution must be considered as unproved, there being no positive evidence in favor of it, but much that is negative against it. As Julian Huxley says: "Lamarckism is self-contradictory, since it maintains that 'a past of indefinite duration is powerless to control the present, while the brief history of the present can readily control the future.'"—Ray Lankester.

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CHAPTER XII

ORTHOGENESIS AND KINETOGENESIS

Of the several hypotheses to account for the origin of species which are opposed or supplemental to the Darwinian factor of natural selection, two stand out sharply as of great importance, if they are finally found to be true. This proof can only be established by impartially conducted observations and experiments extending through years to come. At present the mass of evidence which can be offered in favor of each is to some extent nullified by other well-attested facts, and so the matter stands *sub judice*. Of these hypotheses that of orthogenesis stands first, although it is not an explanation of evolution but a statement of possible fact.

Orthogenesis

Orthogenesis (Gr. *'ορθός*, straight, and *γένεσις*, production) is the assumption that variations and hence evolutionary change occur along certain definite lines impelled by laws of which we know not the cause. Thomson says of it: "We must be on our guard, however, against the possible fallacy of concluding from the apparent orthogenesis in fossilized and surviving stages that there was no zigzagness and pruning in the process. Types may have had their waywardness gradually sifted out of them."

Orthogenesis has been proposed in explanation of several phenomena for which natural selection seemingly cannot account, such as:

1. The beginnings of advantageous modifications by the selection of individual variations occurring in every direction of change, for it is evident that unless a character appeared at once in a degree of development to give it "selection value" it would be difficult to account for its beginning. But the teaching of the Neo-Darwinians postulates the selection of minute random variations as well as such saltations as the idea just stated would imply.

2. Disadvantageous structures or degrees of development, such as structures which have apparently evolved along fixed and seemingly not advantageous lines, and the development of parts beyond

the point of greatest usefulness, even so far as to lead to individual death or racial extinction. Paleontology reveals to us repeated instances of the evolution of characters which lead on to extinction, such as the huge, unwieldy size of the sauropod dinosaurs; the growth of excrescences, observed in the armored and horned dinosaurs, and, later in time, in the Irish deer (*Cervus megaceros*); the uncoiling of the shell-bearing cephalopods (ammonites and nautilids): all of which are examples of development along disadvantageous lines or to disadvantageous degrees. When these are observed in a race a wholesale thinning of the ranks, if not final extinction, may be confidently predicted. Natural selection implies racial improvement, and the development of advantageous, not detrimental, structures; hence the theory of orthogenesis has been proposed to account for the latter as well as the former.

3. Degeneracy and the loss of structures. As we have seen, the reversal of natural selection would account for the elimination of a character formerly useful but which, in altered circumstances, has become a positive menace to survival. On the other hand, if the structure becomes merely valueless, cessation of selection would account for its diminution but not for its utter elimination. Orthogenesis has been offered as a supplementary explanation here.

Explanations of Orthogenesis

The two principal explanations of orthogenesis, those of Naegeli and Eimer, have been stated by Newman:

"Carl von Naegeli's ideas . . . involve a belief in a sort of mystical principle of progressive development, a something, quite intangible, that exists in organic nature, which causes each organism to strive for or at least make for specialization or perfect adaptation. . . . Naegeli believed that animals and plants would develop essentially as they have without any struggle for existence or natural selection. Hence this form of the orthogenesis theory is . . . alternative to natural selection."

Theodore Eimer's explanation is more scientific and less mystical than Naegeli's. "He believed that lines of evolution were not miscellaneous and haphazard but were confined to a few definite directions, determined at their initial stages not by natural selection but by the laws of organic growth, aided by the inheritance of acquired characters. A new character makes its beginning as

would the first step in a slow chemical change, or series of such changes, and it must go through to a fixed end, under given conditions, just as surely as does the chemical process. Only when a given character or line of evolution results in the production of a very positive advantage or disadvantage to the species does natural selection step in to interfere with orthogenesis. The causes of orthogenesis are said 'to be in the effects of external influences, climate, nutrition or the given constitution of an organism.' Natural selection is therefore subordinate but not dismissed."

Orthogenesis Contrasted with Ortho-Selection.—At first sight there seems to be no real distinction between orthogenesis and descent controlled by selection, as the latter must also lead to evolution along certain definite lines; in fact, it can produce no other kind of evolution. Where modification is the result of the elimination, through the selective struggle, of all other lines of variation, it may be called ortho-selection. In orthogenesis, however, the lines of variation are presumed to be predetermined; hence the resultant lines of evolution are also.

Positive Evidences for Orthogenesis

1. **Parallelisms.**—Analógous or parallel variations are of frequent observation. They are the modifications of similar character which appear in different branches of the same large group or in unrelated groups, although in the latter case they are often called convergences. Comparative anatomy has revealed many examples to show that modifications in a definite or determinate direction may be seen in all the sub-groups of a large family, although appearing in varying degree in different species. Examples are the total reduction of the side toes among the artiodactyls which has occurred in several unrelated genera, such as the giraffe, camel, and prong-buck (*Antilocapra*). A still more remarkable instance would be the parallelism which existed between the pseudo-horses of South America and the true horses of the northern hemisphere, both lines showing a three- and finally a one-toed condition owing to the progressive shortening of the lateral digits and proportional strengthening of the middle one (see Fig. 21). In this instance the relationship is quite remote, although both races belong to the ungulate group.

2. **Over-specializations** are the numerous "excessive structures" which are developed far beyond the limits of usefulness. Such, for

example, are the tusks of the wild hog (*Babirussa alfurus*), the huge horns of the "big horn" sheep, or the enormously elongated and slender neck of several weevil- or snout-beetles like *Apoderus tenuissimus*. One of the dolphins, *Mesoplodon*, has a mouth which can be opened but a little way when the animal is full grown, because a lower tooth grows around the upper jaw on either side. Such excessive structures, which have probably contributed to the extinction of many former species, include among others the tusks of the Jefferson mammoth and the antlers of the Irish deer.

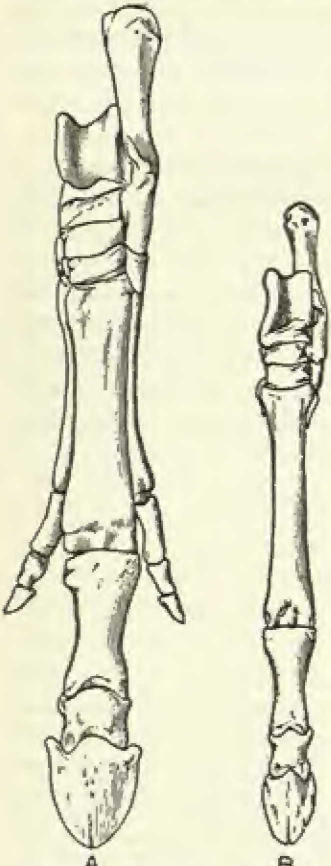

FIG. 21.—Hind feet of pseudo-horses. A, three-toed *Diadiaphorus*, Miocene of South America; B, one-toed *Thoatherium*, Miocene of South America. One-half natural size. (After Matthew.)

3. **Constitutional Limitations on Variation.**—The constitution, or actual chemical composition of the body, permits, as a rule, changes only in a few directions. The breeder of animals or plants may not always produce any desired form or color. "No one has yet succeeded in producing a blue *Maiblume*, a grass with divided leaves, a hen with a parrot's beak." And we can be confident that a notochord can never appear in a beetle. The fact that an animal belongs to a given group renders the possibilities of variation distinctly, sometimes very narrowly, limited. "In this connection it should be mentioned that some biologists have seen in this restriction of the range of variation which inevitably accompanies specialization an important factor in the determination of lines of descent.

4. The correlations which bind each organ to others also restrict the range of variation.

5. Facts from Paleontology Supporting Orthogenesis.—Many facts of paleontology seem to prove the existence of orthogenetic evolution. Wherever sufficient material permits the working out of a phyletic series, we always see a comparatively limited number of lines of development, which, except for occasional lateral branches, run essentially in straight lines, in gradational steps. Such for example are seen in the fossil horses (see Chap. XXXVI).

The cusps of teeth in the mammals afford interesting instances of orthogenesis, as they emerge complete and do not depend upon use for their production; in fact, use destroys rather than perfects them, yet they appear independently but always in an adaptive position in many orders of mammals. From observing the initial trend the ultimate tooth pattern may be often accurately predicted.

Osborn's exhaustive study of the titanotheres, a group of huge Tertiary perissodactyls, has led to many important generalizations. He says:

"Every known step of this transformation [of the titanotheres] is determinate and definite, every additional character which has been observed arises according to a fixed law and not according to any principle of chance.

"In *eleven* principal branches which radiate from the earliest known forms (*Eotitanops gregoryi*) of this family, exactly similar new characters arise quite independently at different periods of geologic time which are separated by lapses of tens of thousands of years.

"In certain branches the horns appear thousands of years later than in others and after their appearance may exhibit a singular inertia, or lack of momentum, over a long period of time. Every character has its own rate of velocity both in individual development and in racial development [evolution]."

"The phyletic series . . . of recent species also show, where we are able to trace them, distinctive single lines of development" (Kellogg).

Kinetogenesis

Cope's theory of kinetogenesis or "mechanical genesis" has been accepted so widely, especially by paleontologists and pathologists, that it should be studied in some detail, with the vital objections which have been raised against it.

The word *kinetogenesis* (Gr. κινητός, movable, and γένεσις, production) is thus defined: "The doctrine or hypothesis that animal structures have been produced directly or indirectly, by animal movements." Cope's arguments, especially as applied to

the vertebrates, are based upon the following: The vertebrates present two distinct advantages. First, we have a more complete paleontologic series. Second, we have the best opportunity for observation and experiment on their growth processes, since we ourselves and our companions of the domesticated animals belong to this branch of the animal kingdom.

Mechanics of the Vertebrate Skeleton

Abnormal Articulations.—Many of the data for experimental work are found in the records of surgery, and from this source inferences have been drawn as to the construction of normal articulations. Experiments have shown that in the case of unreduced dislocations or permanently bent joints certain predictable changes will always occur. That portion of the articular cartilage which fails to meet its fellow either throughout because of a limitation of its movement, or through dislocation so that it only comes in contact with the soft parts, is permanently destroyed and, under certain conditions, a new articulation may be formed where a permanent displacement of the joint has occurred.

The great plasticity of bone was the basis for the wonderful bloodless operation for the reduction of congenital hip dislocation invented by the famous Viennese surgeon, Doctor Lorenz, and demonstrated in America some years ago. In this operation, the dislocated thigh-bone itself was made the instrument, pulled from the abnormal socket which had been formed, and the head, being placed in the partially occluded normal socket, was forcibly ground into it. This always results in the destruction of bony tissue in the motionless bone. The femur was then bound firmly in place until, through the resorption of unnecessary material and the rebuilding of bone where it was needed, the socket was restored to its original form, and then induced movement and massaging completed the cure. The operation was successful in a high percentage of cases where performed upon children of tender years.

Even the pressure of soft parts can cause the absorption of bone, as shown by the interior cavity of the skull, which in many instances retains a faithful impression, not only of the general proportions of the brain, but even of its convolutions and of the blood-vessels in its membranous coverings.

Normal Articulations.—Cope uses for illustration particularly the strong complex ankle-joint of the ruminating animals (ox,

deer, camel, etc.) and the horse, in which the motion, while wide in its fore-and-aft range, is restricted to one plane of space, resulting in a treble tongue-and-groove joint which resists dislocation although it may be broken by force (see Fig. 46). The articulation lies between the upper bone of the ankle, the astragalus, and the shin-bone or tibia, the former, which is convex antero-posteriorly, having two keels which fit into corresponding grooves in the concave end of the latter. The lower end of the tibia possesses a single keel which corresponds to a groove between the two astragalar keels. The formation of this joint has been thus explained:

"In all bones the external walls are composed of dense material, while the centers are spongy and comparatively soft. The first bone of the foot (astragalus) is narrower, from side to side, than the tibia which rests upon it (see Fig. 46). Hence the edges of the dense side-walls of the astragalus fall within the edges of the dense side-walls of the tibia, and they have pressed into the more yielding material that forms the end of the bone, and causing bone absorption, pushed it upward, thus allowing the side-walls of the tibia to embrace the side-walls of the astragalus. . . .

"The same active cause that produced the two grooves of the lower end of the leg produced the groove of the middle of the upper end of the astragalus. Here we have the yielding lower end of the tibia resting on the equally spongy material of the middle of the astragalus. There is here no question of the hard material cutting into soft, but simply the result of continuous concussion. The consequence of concussion would be to cause the yielding faces of the bones to bend downward in the direction of gravity, or to remain in their primitive position while the edges of the astragalus were pushed into the tibia. If they were flat at first they would begin to hollow downward, and a tongue above and a groove below would be the result. . . . This inclusion of the astragalus in the tibia does not occur in the reptiles, but appears first in the Mammalia, which descended from them. . . . Every line of Mammalia commenced with types with an astragalus which is flat in the transverse direction, or without median groove. From early Tertiary times to the present day, we can trace the gradual development of this groove in all the lines which have acquired it. The upper surface became at first a little concave; the concavity gradually became deeper, and finally formed a well marked groove" (Cope).

The history of the wrist joint is similar, and in many instances the articulation between the bones of the palm (metacarpals) and sole (metatarsals) with their respective digits as well. This is especially true of forms which, like the speedier ungulates, have elevated the heel and wrist off the ground and walk upon the modified claws, the hoofs. Where the foot is supported by a yielding

pad, as in the camels, the keels at the ends of the metapodials are incompletely developed, as their purpose, where present, is to keep the toes from spreading, and a yielding foot is a necessary part of the desert adaptation which the camels so admirably illustrate (see Chapter XXXVII).

Vertebral Column.—The vertebral column among vertebrates, especially among terrestrial types, is a marvel of mechanical design. Aquatic adaptation relieves the backbone of the creature's weight, and hence the vertebræ tend to retain or re-acquire primitive simplicity of structure. The articulations of the vertebræ one with another are effected by the faces of the adjacent centra (see Pl. XI) or by the additional articular facets, borne on the neural arch, known as zygapophyses. The reptiles exhibit the greatest variety of articulations, except those of the zygapophyses which are fairly uniform, while in the mammals the modification of each group of articulations is equally striking.

The forms which the articulations of the centra assume are four in number: first, the amphicœlous (Gr. ἀμφί, at both ends, and κοῖλος, hollow, said of vertebræ in which both ends of the centrum are concave); the ball-and-socket, which may be procœlous (Gr. πρό, before, concave in front) or opisthocœlous (Gr. ὄπισθεν, behind, concave behind); the plane or amphiplatyan; and the saddle-shaped, in which the same face of a given vertebra is at once concave in one dimension and convex in the other. Of these various sorts the first is chiefly distinctive of fishes and certain Reptilia (ichthyosaurs), while among mammals it is imperfectly developed, being only a modification of the plane surface and usually occurring in comparatively few vertebræ.

The ball-and-socket type is mainly found in the neck of long-necked reptiles (dinosaurs), in the crocodiles, and in the mammals, where it permits the maximum degree of flexibility. Those mammals (perissodactyls and artiodactyls) in which the ball-and-socket articulation is found in the neck also show it, although in reduced degree, in the vertebræ of the loin, while the thoracic vertebræ exhibit a tendency in the same direction. The saddle-shaped articulation, while characteristic of the neck vertebræ of birds, is present in the mammals only in certain genera of monkeys. The majority of Mammalia have plane articulations on all of the vertebræ. In those forms in which movement of the vertebræ upon one another has become impossible, the centra coössify or fuse together,

as in the region known as the sacrum, where a variable number of vertebræ, depending upon the length of the ilia or hip-bones, unite to form a firm structure which is solidly articulated with the pelvic girdle. Among birds this coössification is apt to extend still further, in some instances including practically the entire trunk, while in the whales, the form of whose body renders any independent movement of the head impossible, the neck is much shortened and the vertebræ, especially in the whale-bone whales, unite into a solid mass of bone.

There is, in all of this, abundant evidence of the effects of use and disuse, the ball-and-socket joints being developed where the greatest all-round flexibility is characteristic. This is therefore the prevailing type of articulation among Reptilia, the degree of its development being in direct proportion to the weakness of the limbs, for in the large and long-limbed terrestrial dinosaurs the articulations of the trunk and to a less extent of the tail vertebræ tend to become plane. In the mammals it is best developed in the most flexible regions, the neck and loin. The saddle-shaped articulation also permits considerable flexibility, but mainly in the vertical and horizontal planes. The fact is that in the ancestral whales the neck was considerably longer than in their modern descendants and had its centra distinct, the shortening and final coalescence of the centra arose with the gradually increasing powers of locomotion through the water, which would enable the creature to overtake and capture its prey without the necessity of using a long, darting neck to seize it in the pursuit. The contrast is strikingly illustrated by the whale-like ichthyosaurs among reptiles on the one hand and the plesiosaurs on the other (see Figs. 55, 58). In the former as in the whales the tail became the principal organ of locomotion with, in all probability, a corresponding increase of speed, whereas in the plesiosaurs the more laborious method of propulsion by the paddle-like limbs made the speed of the creature as a whole considerably less and necessitated a proportionately longer and more flexible neck analogous to that of the fish-eating alligator snapping turtle (*Macroclemmys temmincki*). Of this vicious beast Agassiz says: "It does not withdraw its head and limbs on the approach of danger, but resorts to more active defence. It raises itself upon the legs and tail, highest behind, opens the mouth widely, and throwing out the head quickly as far as the long neck will allow, snaps the jaws forcibly upon the assailant, at the

same time throwing the body forward so powerfully as often to come down to the ground when it has missed its object."

The wonderful complication of the axial mechanism is shown in its highest perfection in certain of the dinosaurs, for never before nor since has nature produced such mighty animals unsupported by an external sustaining medium. In one of the most remarkable of these forms, *Diplodocus* (see Chapter XXX), we have an animal of relatively short body borne on massive column-like limbs and with an extremely long neck and tail, the former of which was evidently a very mobile and self-sustaining organ, while the latter, though capable of considerable movement and self-support, probably was either largely water-borne—for the creature was at least semi-aquatic in its habits—or may have dragged on the ground when the animal came ashore. The entire fabric of the vertebral column is a marvel of lightness and ingenuity of design. The great mobility of the neck is indicated by the highly developed (opisthocœlous) ball-and-socket central articulations, but especially by the extreme lightness of the centra themselves, which are pierced by deep lateral cavities leaving a median dividing wall so thin as to be readily broken through. This mobility is also shown by the complexity of the indicated musculature, for the points of muscle attachment are well developed and numerous keels and buttresses running obliquely in both directions across the centra and neural arches show the lines of stress not of few massive muscles but of numerous smaller muscles and tendons. Moreover, the neural spines, which are usually single, are here deeply cleft from the third cervical back to the sixth dorsal, indicating the pairing of the great muscles which run along the mid-dorsal line of the neck and back, and the independent action of the two members of the pair. This of course is indicative of a wide lateral sweeping of the neck and head.

In the dorsal region the faces of the centra flatten, indicating little flexibility unless the centra were separated by thick compressible pads of cartilage, a supposition which the articulation of the zygapophyses does not bear out. Here, except for the development of deep lateral cavities (pleurocœles) in the centra, the vertebræ are relatively simple, indicating a similar simplicity of the musculature. The sacrum is a massive structure consisting of three closely coalesced vertebræ united not only by their centra but by the neural arches and even the dorsal spines, and a fourth vertebra the spine of which is free, although the centrum is well coössified

with the others. This last vertebra is interpreted as a caudal which age and lack of mobility have caused to unite with the vertebræ in front. The sacrum is the fulcrum of the whole wonderful lever, and the coalesced spines afford a firm anchorage for the long muscles and tendons which run forward toward the neck and backward to the tail—the tension members of the fabric. The sacrum is very solidly fastened to the hip bones or ilia by massive processes which extend outward and backward and unite distally into a heavy roughened plate forming the abutment against which the ilium bears. The hip socket is large and thoroughly braced by this bony plate and the bone (peduncle) extends downward in front of the socket in such a way as to meet the thrust of the thigh in ordinary standing posture, in walking when the hind limb is used to urge the animal forward, and also if the creature reared on its hind legs, evidently a very feasible act when the body was partially water-borne. The obliquity of the transverse processes which has already been described is such as to meet this unusual strain.

The tail lacked the great flexibility of the neck, but must have been capable of some lateral movement as well as a certain amount of elevation. The centra are again lightened but are by no means as complicated as are those of the neck. The transverse processes, especially on the anterior vertebræ, are widely expanded plates of bone, indicating powerfully developed lateral muscles. The tail must have had three uses: for swimming, somewhat as a serpent swims, a movement which requires a certain flexibility but does not perhaps necessitate the extreme range of the food-getting head and neck; for defense, for the only visible weapon of which the creature stood possessed was some ten feet of slender whiplash-like terminus to its tail, comparable to that seen in many modern lizards and serving as a very efficient flagellant for the punishment of would-be offenders against the owner's person; and for temporary support when the animal reared the fore quarters aloft. That this last need may have occasionally arisen is still further attested by the occasional abnormal coalescence of two of the caudals as in the great specimen in the Carnegie Museum at Pittsburgh. These vertebræ, the estimated seventeenth and eighteenth, are at about the point where the tail would meet the ground in such a manœuver. To gain a full appreciation of all this, it should be borne in mind that *Diplodocus* was one of the giants of geologic time, stretching its mighty length through a

span of eighty feet or more, of which some sixty-five lay without the pillar-like supports, and therefore, except for the resting of the tail upon the ground or the support given by the water when submerged, the neck or tail must each have been capable of being sustained by a single end.

There is a wonderful freedom of design in the construction of the individual vertebræ comparable to that seen in Gothic architecture, for not only is each vertebra different from its fellows but even the two sides of the same bone may be unlike. The whole structure of the *Diplodocus* skeleton is so perfect a response to the multitudinous stresses to which its various elements have been subjected that to one who can appreciate the design of a bridge or building or any other sustentative fabric the conclusion that it is the result of mechanical genesis is almost irresistible.

Tendons which have the minute structure of bone are often preserved in dinosaurs, notably in the iguanodons of Europe and their American relatives, camptosaurs and hadrosaurs (Chapter XXXI), and here the lines of tension are beautifully indicated just as the keels and buttresses of the vertebræ give evidence of lines of compression.

Limb Proportions.—Limb proportions also follow definite mechanical laws which at first seem curiously contradictory, for both impact (compression force) and strain (extension force), while opposite in their action, have the same effect upon bone, that of causing it to elongate in the line of the stress. Transverse stress, on the other hand, would cause growth at right angles with the length of the bone.

Speed adaptation generally results in the elongation of the two lower segments of fore and hind limb and the relative shortening of the upper, while relatively slow progression as in the elephant gives rise to a lengthened proximal segment, that nearest the body, the distal one remaining relatively short (see page 269). With the apes, such as the gibbon, in which most of the progress from branch to branch and from tree to tree is sustained by the arms, the latter are enormously elongated as compared with the legs, which are of relatively less use and are proportionately very short, so that when the ape stands with the body practically erect the knuckles still touch the ground (see Pl. XXVII). A regular gradation has been shown by Huxley to exist between these extremes and that in terrestrial mankind, in which the legs are the longer,

the orang, chimpanzee and gorilla representing the intermediate stages in the order named, the last standing nearest to man. If man's legs are longer than his arms as a result of their greater use, their growth stimulus was *impact*, whereas with the gibbon's arms which are the longer the stimulus was a *strain*. The tree sloths (see Figs. 65, 66) also have greatly elongated proximal segments to the limbs, the hands and feet being reduced to curious structures terminating in immense hook-like claws. The huge Pleistocene ground sloths, on the contrary, although retaining enough arboreal characteristics to point to a partial tree-dwelling ancestry, had comparatively short and ponderous limbs, but the relative lengths of limb-segments were retained. (See Pl. VI.)

Archelon, the giant turtle from the Cretaceous of South Dakota, mounted in the Yale Peabody Museum, had suffered mutilation during life, for the right hind foot is missing and the condition of the lower leg bones, which lack their distal end, is pathologic. The most interesting feature, however, is the difference in size of the two thigh bones, that of the perfect left limb being materially larger than that of the crippled right, showing the result of the cessation of growth-stimulus with the loss of utility. But this is an ontogenetic instance and could not, so far as our knowledge goes, become evolutional; the other instances which are constant and predictable are the result of evolutionary processes, whatever they may be. Cope and others have taken many other instances, such as the modification of form into radial symmetry for sedentary types and bilateral for the locomotor, the mechanics of the teeth, of muscular development, of the shells of invertebrates; but enough have been given to show that numerous modifications of animals *conform* with mechanical laws whether mechanics is the prime mover in their production or not.

Objections to Kinetogenesis

Several arguments have been offered by the opponents of this theory of which the most important are: First, the apparently illogical and self-contradictory assumption that stimuli of different kinds produce similar results, while stimuli of the same kind may produce different results. Experiment, however, has proved the truth of this apparently paradoxical statement, for the irritation of bone will produce either bone deposits or bone absorption according to the degree of irritation. Thus moderate stimulus, such

as the pressure and stretching mentioned above, may stimulate growth. Continued heavy pressure, on the other hand, causes bone absorption at the point of contact.

A second objection which has been made to kinetogenesis is that if growth-stimulus exist, how can there be a limit to increase, so long as the stimulus of use prevails? This objection is met by the assumption that the stimulus is stress due to disharmony between an organism and its environment, and that kinetogenesis is the result of the effort on the part of the organism to overcome this lack of harmony. When the organism is sufficiently adjusted to meet the requirements of the environment, equilibrium is attained, the stress is reduced to the point necessary for the maintenance of the mechanism in working condition, and further growth ceases. In easy circumstances, where little or no exertion is necessary, there is not even sufficient stimulus to raise the mechanism to a state of efficiency, and the degeneracy of disuse results.

Despite Cope's arguments, this is one of the objections to his theory which is most emphasized by its opponents. It will at once be seen that even if the objections above are met, a third will yet remain, that of the acceptance of the Lamarckian factor of the inheritance of acquired or ontogenetic modifications, upon which the whole doctrine of kinetogenesis seems to depend for its inclusion among the potent factors of evolution.

Osborn's Theory of Coincident Selection.—This objection Osborn has striven to avoid by his idea of "coincident selection," which he states as follows: "Individual or acquired modifications in new circumstances are an important feature of the adult structure of every animal. Some congenital variations may coincide with such modifications, others may not. The gradual selection of those which coincide (coincident variations) may constitute an apparent inheritance of acquired modifications."

Although these may occur they would hardly seem sufficient to account for the host of mechanical adaptations which exist. Many of these may be ontogenetic, recurring in successive generations through the influence on each individual of similar conditions with resultant similar adaptations. An illustration would be the tanning of the skin upon exposure to the sun in an otherwise fair individual. This would be repeated in each successive generation as an ontogenetic modification. Ultimately a germinal variation in the direction of greater swarthiness might occur. As this is a distinctly

advantageous variation in those exposed to the harmful rays of the sun, Natural Selection would at once intervene to perpetuate it. Thus the ontogenetic modification, while not in itself heritable, would serve as a safeguard until the germinal variation coinciding with it could be established.

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PART III

THE EVIDENCES OF EVOLUTION

SECTION I. ONTOGENY

CHAPTER XIII

THE LIFE CYCLE

The marvel of life is nowhere more wonderfully displayed than in the development of the individual plant or animal from its minute beginning; and the continuation of its life in offspring which in turn undergo their mortal span, handing on their life to other generations yet unborn, adds to the wonder. Man, through his intelligence, and as a result of his inventive research, has made many marvellous things, and some of his creations are little short of miraculous. Take, for example, the most intricate product of human manufacture, a battleship, into which thousands of tons of steel and other material have been fashioned, forming a fabric more complex in its gross anatomy than any created being, of huge size and great speed, with armor to protect its vitals, and guns whose projectiles leave their muzzles at a velocity which would, if continued, belt the globe in half a day, dealing death and destruction to others like itself beyond the limits of the horizon, capable of combating the elements, safe alike in calm or storm, and possessing, as every sailor knows, individual characteristics which seem almost animate. But this marvel is after all a mere mechanism, the product of human skill in design and fruition, and between it and the simplest of nature's children there is a great gulf fixed which human intelligence will never bridge. For organisms possess the powers of self repair and procreation and can hand on their life and characteristics to their children, while the mechanism will sooner or later reach the end of its being and nothing will be left of it but a pile of wreckage and a memory.

The Life Cycle

Several distinct stages are recognized in the career of any organism, certain of which constitute the life cycle. They are, briefly enumerated, the egg, embryo, adolescent, and adult, which in turn gives rise to the egg of a future generation. An additional

stage, not always included, is the senile, or that of old age, and the life of the individual is terminated by death, which, however, although a perfectly normal phenomenon, is not necessarily part of the life cycle and may occur at any stage of the organism's career. If death occurs before procreation is accomplished, the normal life cycle is not complete, for, as the name *cycle* implies, the full sequence of events is from egg to egg, or if the individual be a male, from egg to sperm.

Egg.—The egg, germ, or spore, is the initial stage in the ontogeny of any organism unless it be asexually produced, and perhaps the greatest marvel of the organic world is the minuteness of this starting point, for while an ovum the size of a pin-head is a large one, many are microscopic, and a spermatozoön may be but $\frac{1}{100,000}$ of the ovum's size! And these two uniting cells are the vehicles of inheritance and contain within them all the future characteristics, physical, mental, and moral, wherein the offspring resembles its parents, be they rotifers, or dinosaurs, or mice, or men! But this is not all, for Delage cut a very minute sea-urchin's egg into three parts, and reared a larva from each, and in another experiment he reared an embryo from $\frac{1}{37}$ of a sea-urchin's egg. Twin animals may often be obtained from one ovum by effecting a separation of the first two cleavage cells, and it is known that this is the way the so-called "identical" human twins are normally produced. Professor E. B. Wilson, by shaking apart the four-celled stage in the development of the lancelet, caused the production of quadruplets.

On the other hand, the eggs, especially of reptiles and birds, are relatively enormous, because there is contained within the shell sufficient food in the form of "yolk" to sustain and build up the organism through its entire embryonic period. The maximum recorded size of an egg is that of the recently extinct flightless bird, the æpyornis of Madagascar, the shell of which measures 9 by 13 inches, while an ostrich's egg measures but $4\frac{1}{2}$ by 6. The æpyornis egg would therefore hold the contents of 6 ostrich eggs, or 148 hen's eggs, or 30,000 humming bird's eggs (Lucas). There is rarely a very definite ratio between the size of the egg and the creature which produced it, for the apteryx, another flightless bird still living in New Zealand, whose bodily bulk is less than that of a hen, lays an egg measuring three by five inches and weighing about one-third of its own weight. It is not surprising, therefore, that it lays but two.

The presumption is, until we have evidence to the contrary,

that, in common with most other reptiles, except the viviparous ichthyosaurs whose high-seas adaptation rendered it impossible to come ashore for egg-laying, and a few modern lizards and snakes, all dinosaurs were probably egg-laying. If so, the eggs of a 67-foot *Brontosaurus* must have been huge, although even they may not greatly have exceeded those of the æpyornis.

Embryonic Stage.—This is the period of development from the beginning of cleavage until the assumption of free life, generally that spent either within the egg-shell or within the body of the mother if she is viviparous as in certain sharks, the above mentioned reptiles, and the mammals. Certain stages of development are common to all metazoan animals and the inference is therefore that these must represent ancestral stages through which the Metazoa as a whole passed in the dim youth of their racial career.

Immediately after impregnation, cleavage occurs, dividing the egg into two, then four, then eight, sixteen, and so on, individual cells which remain attached to one another, forming a solid aggregate known as the morula (dim. of L. *morum*, mulberry). Further segmentation produces a hollow embryo, the blastula (dim. of Gr. βλαστός, sprout), the cavity within being the segmentation cavity or blastocœle (Gr. κοῖλος, hollow). The organism now consists of a single layer of cells enclosing the more or less voluminous cavity. In its simplest form the blastula shows no cell differentiation, but in the aquatic invertebrates it may be uniformly ciliated and swim freely through the water with a rotary movement about a definite axis, one end of which always points in the direction of progress. In many blastulæ, especially such as are not free-swimming, the cells soon begin to differentiate, at the posterior pole of the free-swimming forms or at the corresponding portion of those which are non-motile. These posterior cells are generally somewhat larger than the anterior ones, especially in those embryos in which much food-yolk tends to concentrate, and they will ultimately give rise to the vegetative tissues of the organism. The next stage is that known as the gastrula (dim. of Gr. γαστήρ, stomach), in which the embryo becomes two-layered, with a full differentiation into two distinct tissues composed of cells, the primary requisite of a metazoan animal. This is generally the result of an inpushing or invagination of the cells of the vegetative pole into the blastocœle, more or less obliterating it. The embryo is now a two-layered or diploblastic sac, the newly

formed cavity lined by the invaginated cells being the primitive gut or archenteron (Gr. ἀρχ-, first, and ἔντερον, intestine), while the opening to the exterior is the gastrula mouth or blastopore. Of the two primitive germ-layers now formed, the outer one in the higher Metazoa gives rise to the integument, nervous system, and sense organs of the adult and is known as the ectoderm, while the inner one, from which the digestive tract and certain of its glands, such as the liver, develop, is known as the endoderm (see Fig. 22).

Up to this point all metazoan development, whatever the ultimate result, follows the same or strictly parallel roads, although

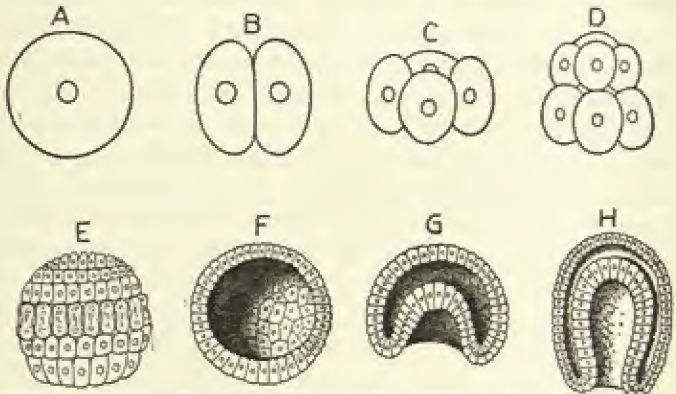

FIG. 22.—Stages common to all Metazoa. A, egg; B, C, D, cleavage stages; E and F, blastula; in F, which is somewhat older than E, one-half has been removed; G, beginning of gastrular invagination; H, complete gastrula. G and H sectioned as in F. (After models of *Amphioxus* by Hatschek, from Wilder.)

the exigencies of its life, causing the animal to be sedentary or free, and especially the presence and amount of food yolk may modify the several stages to a considerable degree. Now we come to the parting of the ways, when the least related go each their several roads, which ultimately branch into as many byways as there are forms of life. The nearer of kin the creatures are, the later is their embryonic divergence.

Post-embryonic Life.—The *adolescent stage* is the period of youth, from the time when the embryonic stage is left until sexual maturity is attained, when the organism becomes an adult, even though its growth shall not have been completed. Often the young, once the embryonic stage is past, is a miniature of its par-

ents, again it may differ from them so widely that its relationship to those who gave it existence would never be even guessed. In the former case the development is direct, in the latter indirect or by metamorphosis, the adolescent form being called a larva.

A familiar instance of metamorphosis is that undergone by the frogs and toads, in which the young hatch out as limbless, tailed larvæ with tuft-like gills on either side of the neck. The head is not constricted off from the body and the long tail bears a delicate web of skin above and below which aids in swimming. The mouth is armed with a pair of horny jaws composed of numerous closely-set horny teeth. In the course of a few weeks, in some species, the limbs begin to appear, first the hind limbs, later, apparently suddenly, the fore. In reality the fore limbs have been developing all along, but were concealed by a fold of skin, the operculum, which had previously grown over the gills. Later the creature's lungs become functional, the tail shrivels, and it soon emerges on land as a perfect frog or toad as the case may be. There are all sorts of modifications of this straightforward process, due to adaptations to various life conditions, but the fact of metamorphosis remains, although in some instances approaching very near to direct development.

The frogs are instances of metamorphosis from a lower to a higher plane of life and most of the marvellous insect metamorphoses are of a similar sort; but the change is not always progressive upward, and in some instances, notably where the adult is sedentary or parasitic and as a consequence degenerate, the metamorphosis is retrogressive and results in an adult animal on a distinctly lower plane than when in the larval stage. The chapter on parasitism and degeneracy (see Chapter XVII) will give several instances of this retrogression, and a single instance, that of the tunicates or sea-squirts, will suffice for the present.

These animals (see Fig. 23) are in part planktonic, but mostly sedentary benthonic forms, having a somewhat sac-like shape, with two orifices, one inhalant, the other exhalant, through which water enters and leaves the body for the purpose of food-getting and respiration. Though chordate animals, the adult shows but one of the three diagnostic characters which serve to define the group. This is the pharynx perforated by gill-slits, the notochord and the typically hollow nervous system not being in evidence. They are present in the young, however, for there hatches from the egg a

tiny tadpole-like creature which swims around in the sea by means of a webbed tail stiffened by a gelatinous notochord. There is also a hollow spinal cord, somewhat like that of the frog tadpole, except that there is a very slight dilatation where one would seek to find the brain and this contains a very primitive sort of eye and another organ which may represent an ear or an organ of equilibration (balancing sense). After a very brief life of freedom the larva becomes fixed first by a pair of adhesive organs and later by the outer "tunic" of cellulose characteristic of the group to which it belongs. The tail, the notochord, the greater part of the nervous system, and the sense organs disappear, and the creature degenerates into a stage of development comparable to that of the lower Metazoa. Were it not for their life history, the place in nature of the tunicates would be very difficult to fix; as it is they are clearly a degraded offshoot of the stem which gave rise to the vertebrates themselves.

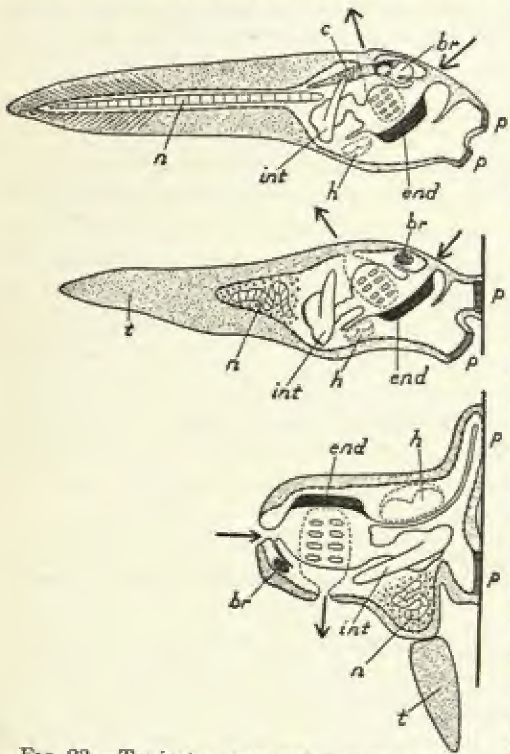

FIG. 23.—Tunicate retrogression from free-swimming larva. *br*, brain; *c*, nerve cord; *end*, endostyle; *h*, heart; *int*, intestine; *n*, notochord; *pp*, adhesive papillæ; *t*, tail. Orientation indicated by arrows which mark incurrent and excurrent orifices. Greatly enlarged. (After Seeliger, from Wilder.)

The *adult stage* is reached as soon as the metamorphosis, if such there be, is completed—with the insects the assumption of the powers of flight marks its advent. While growth may continue for some time, or even, as in certain fishes, almost indefinitely,

the animal is generally sexually mature and parenthood is possible.

Ultimately there comes senility, when the bodily powers begin to wane, procreation ceases, and the animal becomes less and less active and capable of protecting itself. It is thus more readily the prey of disease or of other rapacious forms, and shortly death ends its career. Thompson Seton, who knew animals as few are privileged to do, tells us that among wild creatures practically all die a violent death sooner or later, and that what we call a "natural death" as applied to mankind rarely if ever occurs among them.

Length of Life.—In most organisms there is a definite limit of growth and when the size best suited to the needs of the species is attained further increase ceases. Exceptions apparently exist in certain water-borne forms such as the fishes and whales, where the energy usually needed in overcoming gravity may be turned into growth force and in exceptional cases will produce an individual far in excess of the normal optimum of size. So it is with the length of life. Some organisms which, like the annual plants, die when they have provided for the continuation of their species, have a very definite life span, the limits of which are determined by the procession of the seasons. Others, like the perennial plants, continue to live, barring accident, until sere old age sets in with its warning of impending death.

In those forms with definite life duration, egg-laying is often fatal, for in some animals, as in certain flatworms, there is no birth opening and the young are liberated only through the death and disintegration of the mother. The abdomen of a may-fly bursts during egg-laying and "many female butterflies die after oviposition, and the same is true even of robust animals like lampreys. The drone who succeeds in fertilizing the queen hive-bee dies as he succeeds; all the others who are unsuccessful, also die. A male spider often lays his life on the altar of sex, and the same is true of some scorpions" (Thomson). In creatures which survive there is also a normal duration of life, like man's three score years and ten, which few attain and fewer exceed. Most records of longevity are derived from observations on animals in captivity and hence, as the latter are sheltered from many of the vicissitudes of a wild life, may exceed the average. On the other hand, as for instance in the case of the gorilla, it was formerly impossible to keep a captive alive

for more than a very brief existence, the life of "Dinah," a young gorilla kept in the New York Zoölogical Park for eight months, being once a record. At all events, whether captivity lessens or increases the animal's chance for survival, its length of life cannot exceed the *potential* longevity of its species.

Within each group of animals, the duration of youth is in rough agreement with the possible span of the whole life, and also with the relative size to which the members of the particular species attain, but this is not without some very marked exceptions.

The extreme recorded life duration of insects is that of the American seventeen-year cicadas or "locusts" (*Cicada septendecim*) which in the middle and northern states live no less than sixteen years underground, feeding on the juices extracted from the roots of plants. The spring of the seventeenth year they come out of the ground, burrowing up through the surface soil, and climb the trunks of trees, where they undergo their final moult and emerge as large four-winged bugs. They then pair, the female lays her eggs in slits cut in the twigs of trees, and before the season has waned the adults are at rest, the eggs hatch, the young burrow underground and begin their long subterranean lives. It is interesting to note that thirteen-year broods of what is apparently this same species occur in the southern states, doubtless a response to the longer growing period available in each individual year.

Some recorded instances of longevity are: tortoise 350 years, elephant 130, swan, eagle, and parrot 100, mankind, omitting the biblical patriarchs, 70 years with perhaps 130 years as a maximum, sea-anemone 66 years, horse 42, crayfish 20, and so on; while the recorded age of the giant trees (sequoias), some of which antedate the Roman Empire, gives the greatest known duration. As Thomson says in *The Wonder of Life*, several groups of animals may be recognized from the viewpoint of their life span:

"(1) The first is that of the immortal unicellular animals which [under ideal conditions] never grow old and which seem exempt from natural death. (2) The second is that of many animals which reach the length of their life's tether without any hint of ageing and pass off the scene—or are shoved off—victims of violent death. In many fishes and reptiles, for instance, which are old in years, there is not in their organs or tissues the least hint of age degeneration. (3) The third is that of the majority of civilized human beings, some domesticated and some wild animals, in which the

decline of life is marked by normal *senescence*. (4) The fourth is that of many human beings, not a few domesticated animals, *e. g.*, horse, dog, cat, and some semi-domesticated animals, notably bees, in which the close of life is marked by distinctively pathological *senility*. It seems certain that wild animals rarely exhibit more than a slight senescence, while man often exhibits a bathos of senility. This is due to the fact that the majority of wild animals seem to die a violent death before there is time for senescence, much less senility. The character of old age depends upon the nature of the physiological bad debts, some of which are more unnatural than others, much more unnatural in tamed than in wild animals, much more unnatural in man than in animals. Furthermore, civilized man, sheltered from the extreme physical forms of the struggle for existence, can live for a long time with a very defective hereditary constitution, which may end in a period of very undesirable senility. Man is very deficient in the resting instinct, and seldom takes much thought about resting habits. In many cases, too, there has come about in human societies a system of protective agencies which allows the weak to survive through a period of prolonged senility. We cannot, perhaps, do otherwise; but it is plain that to heighten the standard of vitality is an ideal more justifiable biologically than that of merely prolonging existence. For if old age be then permitted, it is more likely to be without senility. Those whom the gods love die young."

Death is the final and permanent cessation of life functions, and, in higher animals at any rate, seems to be a gradual process even though it may appear to be instantaneous. For although consciousness has ceased and the heart is stilled forever, the various tissue cells gradually succumb to starvation due to the cessation of the blood stream. With some tissues it is more gradual than with others, for instances are recorded of the growth of hair on a body for some time after general death.

Curious instances of suspended animation also occur which in some cases simulate death so closely as to render distinction very difficult. A notable example is that of the bear-animalcules, minute forms related to the spiders and scorpions, some of which live in damp moss, others in fresh or in salt water. Those inhabiting ditches or other fresh-water pools subjected to drying become completely desiccated and are blown about like particles of dust. If by chance they fall into water, however, they become re-ani-

mated, expanding to their former size and taking up their life functions where they laid them down. Many instances of hibernation or winter sleep, especially among cold-blooded forms, are also death-like.

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CHAPTER XIV

RECAPITULATION, EXTINCTION

Recapitulation

The celebrated German savant, Ernst Haeckel, conceived and set forth in the form of a law the wonderful similarity which exists between the life history of any organism and the evolutionary history of the race of beings to which it belongs. This principle, usually known as Haeckel's biogenetic law (morphogenesis of Hyatt), may be stated as follows: The life history of the individual (ontogeny) gives a brief résumé of the evolutionary history of the race (phylogeny). Or, more briefly, ontogeny repeats phylogeny.

While this is in the main true, the phylogenetic record may be falsified in ontogeny in several ways, just as any historical document may lack certain important portions through the accidental or intentional mutilation of the volume, or may have spurious chapters added thereunto by a later hand. In some instances the results remind one of the palimpsests—ancient parchments from which the work of an older scribe has been erased and over the almost indecipherable traces of the ancient writing a new penman has engrossed an inscription of later date. Where the record is essentially correct in recounting in their orderly sequence the historical events, we may compare it to palingenesis (Gr. πάλιν, again, and γένεσις, production), in which truly ancestral characters conserved by heredity are reproduced in development. The introduction of spurious matter may be likened to cænogenesis (Gr. καινός, recent), in which non-primitive characters make their appearance in consequence of secondary adaptation of the young to the peculiar conditions of its environment. The elimination of certain chapters finds its parallel in tachygenesis (Gr. ταχύς, swift), the acceleration of characters which are crowded back further and further into the embryonic life or out of the life cycle entirely.

Palingenesis.—When one considers the millions of years of evolutionary life which have fallen to the lot of all organisms, if, as we believe, they have all evolved out of one primal creation of

life, and compares those untold ages with the brief span of individual existence, he will see that the record is necessarily so greatly abridged as to make a perfect recapitulation practically impossible. Nevertheless the metamorphosis undergone by the common frog may be taken as a fairly typical instance of palingenesis, as there is little evidence in its life history, except in the development of certain larval organs, such as the adhesive suckers, of any material falsification of the record (see Fig. 24).

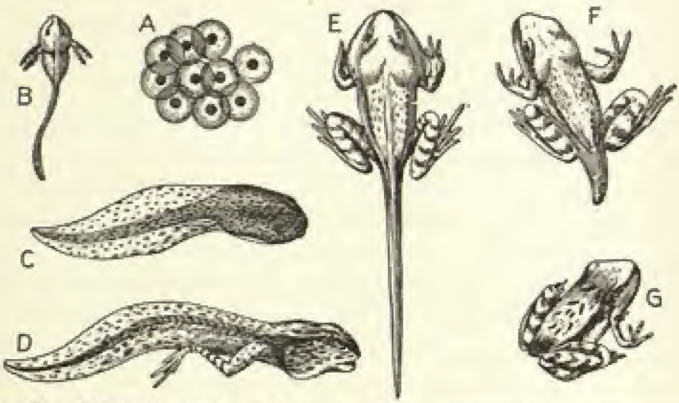

Fig. 24.—Metamorphosis of the frog, *Rana temporaria*. A, eggs, greatly enlarged; B, tadpole with external gills; C, hind legs appearing; D, hind legs well developed; E, tadpole with all limbs free; F, G, stages in which the tail is resorbed, F being a miniature adult. (After Leuckart, from Schuchert's *Historical Geology*.)

The same may be also true of the ontogeny of the lower insects, but as soon as forms like the moths are considered, especially such as have highly adapted larvæ, as in certain of the mimicking forms, it is at once evident that cænogenesis has been at work.

Cænogenesis.—Among the inch-worms, or geometrid larvæ, protective mimicry is common, the creature being elongated and twig-like (see Fig. 25) in form, in color, and in its attitude when disturbed, for it throws itself out rigidly at an angle with the supporting branch to which it is attached by the hook-bearing proplegs at the hinder end of its body. This is clearly an adaptation to meet the vicissitudes of larval life, and the whole insect is very different from the form of a primitive species, such, for instance, as the fish-moth, *Lepisma* (Fig. 113), or *Campodea*, "the simplest living insect." Then, too, the pupa state of the geometrid, in

which the insect passes into a condition of quiescence and the marvellous transformation into the adult takes place, can have no precise parallel in the history of the race, for it is inconceivable that a long period of racial dormancy, during which the evolution of wings was accomplished, could ever have occurred.

Tachygenesis is the rule in ontogeny, and numerous instances might be cited, but certain of the frogs and toads may again be taken as typical instances, for while in most of them the eggs hatch out in water and the young undergo the typical palingenetic development mentioned above, others show all degrees of the suppression of larval stages until metamorphosis is practically eliminated and development from egg to frog is direct.

Fig. 25.—Geometrid larva on a branch. The twig-mimicking caterpillar is the upper right-hand projection from the stem. (From Jordan and Kellogg's *Animal Life*. [D. Appleton and Co.])

"In some the eggs hatch on land, having been laid in holes, on grass or leaves, and when the tadpoles are hatched, they wriggle into water or are washed into pools by the rain. In others, again, the eggs are laid on land, and the tadpoles have lost their gills before they are hatched, but the metamorphosis is completed later on. In a few the complete change occurs inside the egg, and when hatching takes place, little frogs appear, sometimes, however, with a stump of the tail still left. In others the eggs are carried by the parent, and here, too, they may be hatched as tadpoles or as perfect frogs" (Mitchell).

Yet another remarkable life history wherein the strict phylogeny is departed from is that of *Ichthyophys* (Fig. 26), one of the Gymnophiona of the class Amphibia. These are curious, burrowing, snake-like forms with neither tail nor limbs, but which, despite their degenerate specialization, seem to have inherited more of the

characteristics of their ancient stegocephalian forebears than have any other living amphibians. The female of a species which lives in Ceylon and breeds just after the spring monsoon, digs a hole close to the surface near running water where the ground is moist. Here she lays about two dozen eggs, around which she coils herself, probably to protect them against other burrowing lizards and snakes, which are very numerous. During the period of incubation, if such it may be called, the eggs swell to twice their former size, and the mature embryo weighs four times as much as the newly laid egg. The embryo has external gills, which, however, have lost their primal function of respiration for that of nutrition, for they move up and down in the fluid of the egg. The lateral line sense-organs develop, organs of prime importance to all aquatic vertebrates but here functionless while within the egg, which may also be said of the fin developed by the short tail. When the embryo has reached a length of about seven cm., the gills begin to shrink, and at the same time one pair of gill-clefts appears at the base of the third external gill. When the larvæ are hatched, the gills are lost and the young animal takes to the water in a gill-less state, although at the bottom of the aperture on either side two gill arches may be seen, and the larva frequently comes to the surface to breathe. The lateral sense-organs and tail fin now fulfill an important function. The creatures seem to live a long time in the larval stage, but at last the gill-clefts close, the tail fin is lost, the skin assumes a totally new structure, and the fish-like larva turns into a burrowing creature which readily drowns when forced to remain in the water. In this instance the most striking tachygenetic features are the crowding of the gills, which might well be of material service to the aquatic larva, back into the embryonic

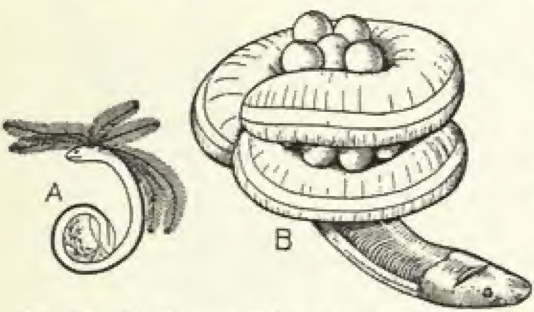

FIG. 26.—Limbless amphibian, cæcilian, *Ichthyophys glutinosa*. A, nearly mature embryo, with gills, tail-fin, and some food yolk; B, female guarding her eggs, coiled in a hole underground. (After Sarasin, from Gadow.)

stage, and their assumption of a different rôle, and the total elimination of any trace of legs from the life history, although the Gymnophiona must have been descended from ancestors possessing limbs.

The Racial Cycle

Students of fossil forms, especially of the molluscs, have come to recognize a series of definite stages in their phylogenetic career comparable to those of the typical life cycle discussed in Chapter XIII. These are as follows:

	Ep-acme		*Acme*	*Par-acme*
Ontogeny	embryonic	adolescent	adult	senescent
	nepionic	neanic	ephebic	gerontic
Phylogeny	phylo-nepionic	phylo-neanic	phyloephebic	phylogerontic

If the life cycle be represented by a curve, the ascending limb will include the nepionic and neanic or what may be called the ep-acme. During the acme the summit of the curve is reached and the organism is in the full fruition of its powers. The par-acme is the period of decadence, when the organism's failing strength is represented by the descending curve terminating in death.

Shells of molluscs, especially of gastropods and cephalopods, preserve the ontogenetic characters, often in a single specimen, better perhaps than the remains of any other group, and have as a consequence lent themselves especially to students of this interesting problem, notably the American paleontologists Hyatt, Beecher, Grabau, Jackson, and J. P. Smith. Not only is this true of molluscs, but in a more or less complete degree of brachiopods, echinoderms, and corals.

In many of the gastropods and cephalopods especially, a single shell of an old individual may have preserved a record of all of the changes it has undergone during the animal's lifetime. Thus we can find at the apex of the coil the tiny embryonic shell or protoconch, then the neanic portion, formed during the animal's youth, simpler perhaps in ornamentation than the adult or ephebic section when the height of development of all of the features, ridges, bosses, spines or complexity of suture characteristic of the species is attained. Then the gerontic or senescent portion is seen, recognizable by an increasing simplicity, comparable to that of the

neanic shell but retrogressive rather than progressive in the assumption of characters. Furthermore, it has been proved by paleontologists that the several stages shown in the development of a given shell reflect the adult condition of more ancient forms, presumably ancestral. Thus, the living *Nautilus*, the sole survivor of a formerly abundant group of cephalopods, has a closely coiled shell, but the earlier cephalopods had not, and coiling was gradually assumed and sometimes secondarily lost in phylogerontic types. In the course of its development, however, *Nautilus* passes through arcuate (L. *arcuatus*, shaped like a bow), loose-coiled, then close-coiled stages directly comparable to the adults of the Paleozoic genera *Cyrtoceras* and *Gyroceras*, and the later *Nautilus* representatives of its own group.

Another highly evolved Cretaceous cephalopod, the ammonid *Placenticeras pacificum*, is characterized in the adult by complex sutures, the lines of juncture of the transverse partitions or septa which separate the chambers of the shell and its outer wall. In the development of its sutures the individual shell passes through simpler stages which are comparable to the adult structures of nautilid and goniatitic forms, followed by stages in which the septa are comparable to those of early *Ammonites* before it assumes its adult generic features (see Chapter XXVI).

In the lamp-shells or brachiopods, the spirally wound buccal (mouth) arms which serve for food-getting usually have an internal limy support which is an outgrowth of the inner wall of the shell. Beecher and others have shown that the stages in development of the exterior and interior of the shell and the brachial (arm) supports can be closely correlated with adult characters of more primitive representatives in the group. As has been said, while stages in development from the young to the adult are all progressive, in senescence the stages that appear are in the main retrogressive. Nautilids and ammonids, which are characterized by close-coiled shells, build loose-coiled or even uncoiled additions; specialized *Ammonites*, with complex septa, in senescence build simple septa, thus assuming simpler characters comparable to those seen in their own youth, and also comparable to the characters of adults in regressive (degenerating) series in their own groups (see Chapter XXVI).

While shell-bearing invertebrates thus lend themselves admirably to the study of recapitulation, vertebrates as a rule do not, for

the skeleton, changing as it does with age, gives only the characteristics of the owner at the moment of death, and one can rarely learn much of the ontogeny from a single individual or the portion of an individual such as is usually available for study. Nevertheless where several individuals of a species are known, or the annually shed antlers of a captive deer (see Fig. 27), enough may be learned to show that the law of recapitulation holds with them as with the invertebrates.

Persistently Primitive Types.—Both plants and animals in nature, as under domestication, show a remarkable variation in plasticity, so that while in the great majority time has wrought wonderful evolutionary changes, with a few it is as though the world stood still and the ceaseless centuries passed over them without effect. In some cases isolation in a remote place, where inter-specific competition has largely diminished, is doubtless one cause of their changeless survival; others are in the thick of the strife but seem to be immune to the influence of changing conditions.

Such, for example, are *Amœba* and the simpler Protozoa and unicellular plants, doubtless relics from the remote Proterozoic age, unless, as seems hardly probable, life evolved from the lifeless more than once and these are the primitive stages of a later creation. *Orbulina* and *Globigerina*, two foraminiferal Protozoa, are known from the Ordovician and doubtless existed long before, while among the Brachiopoda one relic type is *Lingula* and another *Crania*, both dating also from the Ordovician, and persisting practically without change until the present. *Nautilus*, mentioned above, has persisted from the Tertiary, and the family to which it belongs from the Jurassic. Of the vertebrates, an extremely old type is the lung-fish *Ceratodus*, of which a modern derived genus, *Neoceratodus* (Fig. 132), is now found isolated in certain Australian rivers, and which dates from the Triassic. The ancient Port Jackson shark, *Cestracion*, has persisted since the Jurassic and members of its family are found in Lower Carboniferous rocks. In many respects the most interesting relic of all is the tuatera (*Sphenodon*) resident on certain small islands bordering the mainland of New Zealand—a Permian type although somewhat modified from its Paleozoic ancestors. *Sphenodon* is the sole survivor of an important order of reptiles and is of great value to those who would revivify the creatures of other days because of the flood of light which its structure throws on their probable anatomy.

These ancient forms are what are called generalized or primitive, as opposed to specialized types, for they alone can tarry in their evolution while time rings in its changes. High specialization, on the other hand, means a relatively brief career.

Phylogerontic Characters

Just as senility may readily be recognized in the individual by certain characteristics such as the graying of the hair, loss of teeth, of upright carriage, of vigor and elasticity of step, so to the trained eye characteristics are discernible which may point to racial senility. These have been recorded by the English paleontologist, Sir Arthur Smith Woodward, who arranged them under several heads, as follows:

Relative Increase of Size.—One of the characteristics recognizable as belonging to racial senescence, although having no parallel in that of the individual, is relative increase of size far beyond that which is usual in the group to which the animal belongs. In certain recorded instances among the prehistoric animals, such an increase was followed by extinction, and in several living examples racial death is certainly threatened if not a very real probability, for, as we shall see, great increase of size is accompanied by slow maturity and consequent lessening of the rate of increase, which severely handicaps the species in the struggle for existence. An example of phylogerontic immensity is the genus *Productus*, of which *P. giganteus* is the largest brachiopod known, sometimes attaining a width of nearly one foot, while most species hardly exceed one or two inches. *Productus* was very abundant in the Carboniferous and Permian and then was blotted out. The cephalopod *Ammonites* was another relatively huge form, while the living giant squid, *Architeuthis*, is by far the largest known invertebrate, reaching a recorded length of 50 or more feet. Certain of the smaller cephalopods, on the other hand, measure but an inch or two, while between one and two feet would be a fair average for squid.

Among vertebrates the Mesozoic dinosaurs (see Chapter XXX) were truly gigantic, *Brontosaurus* with 67 feet of length and 30 or more tons of weight, but especially *Gigantosaurus*, 80 or more feet long and proportionately heavier, occurring just before the extinction of their suborder; while of carnivorous dinosaurs *Tyrannosaurus*, the culminating form of its race, was the largest and most

terrible flesh-eating terrestrial animal whose existence is thus far revealed. Of living types, we have the giant whales, the sperm, Greenland, and sulphur-bottom, all gigantic compared with the more conservative dolphins and porpoises, and rapidly nearing their extinction. The hippopotamus, exceeding by far all other swine-like animals, is also restricted in numbers and habitat compared with former times, while the elephants are very few to-day, though formerly world-wide in distribution and extraordinarily abundant. Of the old African elephants which reach a stature of 11 to 12 feet, very few are now alive, and the most majestic species of all, *Elephas meridionalis* of Europe and *E. imperator* of America, are extinct. Of primates, the gorilla exceeds all others in size, with the exception of occasional men, and he is now making his last stand against fate in the dismal fastness of the dark continent.

Spinescence.—Another gerontic character found occasionally in all skeleton-bearing animals is spinescence, that is, the tendency on the part of the shells of molluscs and of brachiopods, the external mail of Crustacea, and even the internal skeletons of vertebrates to produce a superfluity of dead matter. In some instances spines and horns are undoubtedly of genuine protective value, or they may be ornamental structures, although the extent to which purely ornamental characters without other practical value to the organism develop in nature is open to question. In general, such excrescences seem like growth-force run riot, as though with the lessening vitality incident to racial old age, it is no longer adequately controlled.

Examples are, among brachiopods, *Spirifer*, in some species of which the hinge-line becomes elongated into spine-like processes, and *Productus horridus*, whose valves are liberally bedecked with spines. Among molluscs there are a number of highly spinescent types, such as the gastropod *Murex* and the bivalve *Spondylus*. Among vertebrates there is a group of lizard-like reptiles, Carboniferous to Permian in distribution, members of the order Pelycosauria, related to the living relic *Sphenodon*, mentioned above. These creatures toward the close of their career were characterized by the enormous elongation of the vertebral spines, which in extreme cases also bore transverse processes like the yard-arms on the masts of a square-rigged ship. *Edaphosaurus* (Fig. 142) was perhaps the most remarkable vertebrate from this point of view. There seems to be evidence that these lengthening spines

were independently acquired in more than one line of descent within this group, but in all cases the appearance of spinescence heralds the extinction of the line.

FIG. 27.—Antlers of stag, showing ontogenetic increase in complexity. Series in the British Museum (Natural History). (From Romanes' *Darwin and after Darwin*. Copyright, Open Court Publishing Co.)

The dinosaur *Stegosaurus* (see Chapter XXXI) shows phylogerontic characters in at least two ways—rapid increase of size over that of allied forms, and a marvellous overgrowth of armor plates and tail spines which heightens the bizarrerie of this most grotesque of beasts. *Stegosaurus* again is the last of its phylum, for no trace of the genus has ever been found in rocks of later date than the Morrison formation which produced it.

The deer are the most familiar recent instance of spinescence in the bony growths known as antlers which surmount the brow. These antlers, which are periodically shed, increase annually in weight, complexity, and number of points until the deer is old, when they begin to simplify again. An interesting recapitulation is shown, for the antlers of a young animal are comparable to those of fully adult Miocene deer, those of somewhat later age to those of the deer of the Pliocene, while a "stag royal" in his prime bears antlers comparable to those of the Pleistocene and Recent deer. Moreover, as one would expect, the deer which attained the maximum development of horns, the great Irish stag or "elk," is now extinct, and we know of no other rea-

son for their extinction than the racial senescence which the antlers imply. The not infrequent interlocking of the horns of two fighting bucks, resulting in their destruction by starvation or the attacks of other animals, shows that the point of greatest utility as weapons of defense and offense has apparently been exceeded, so that the structures are an actual menace to their possessor.

Degeneracy.—Physical degeneracy is another phylogerontic trait, this time paralleling certain senile characteristics of the individual. Among these is *loss of teeth*, which is recorded several times: first, among the fishes such as the sturgeon and certain deep-sea forms like the "gulper" eel, *Macropharynx*, which evi-

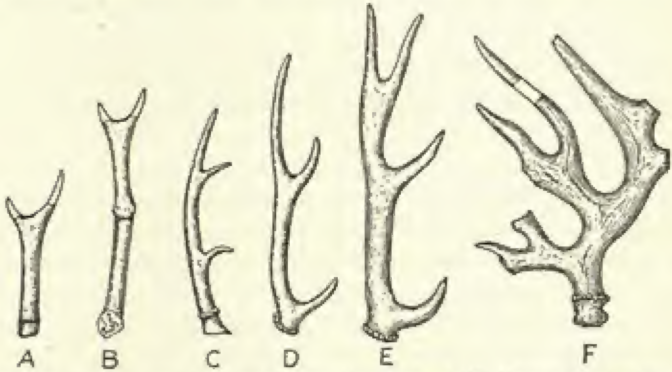

FIG. 28.—Antlers of deer, phylogenetic series. A, B, *Cervus dicrocerus*, Mid-Miocene; C, *C. matheronis*, Upper Miocene; D, *C. pardinensis*, Upper Miocene and Pliocene; E, *C. issiodorensis*, Pliocene; F, *C. sedgwickii*, Pleistocene. (From Romanes' *Darwin and after Darwin*. Copyright, Open Court Publishing Co.)

dently feeds upon the bottom oozes. The turtles, which are among the oldest of living reptiles, had lost their teeth by Triassic time, when they first appear in the rocks; the birds, which were toothed during the Age of Reptiles, have also been toothless since its close. In each of these instances the jaws are sheathed with a horny beak variously modified, so that while the turtles are doubtless fewer than of old, the birds, except for man's interference, can hardly have begun to wane as a whole, although many races are extinct. Among dinosaurs, three phyla were, at the time of their extinction, rapidly losing their dental armament: the sauropod *Diplodocus*, 85 feet in length, whose teeth are slender structures no larger than lead pencils; *Genyodectes*, a carnivorous dinosaur of Patagonia; and *Struthiomimus*, one of the same group from the late Cretaceous of

Alberta and Montana (see Chapter XXX). Mammals occasionally show loss of dentition, notably the very ancient, egg-laying monotremes of Australia and Tasmania and the anteaters among edentates.

Another degeneracy is the assumption of an *eel-like, elongated form* which W. K. Gregory tells us has been acquired no fewer than forty-four distinct times among vertebrates alone. These have been the result of independent or homoplastic evolution, and the criteria which in almost every instance distinguish them are: anguilliform (eel-like) body with multiplication of vertebræ, gephyrocercal tail (tapering to a point), reduced pelvic limbs, and usually predatory habits. Gregory lists three groups of cyclostome fishes, one of sharks, a lung-fish, thirty evolutions among the Teleostomi or bony fishes, three among Amphibia, five among Reptilia, and one group of mammals, a remarkable record.

Extinction

Extinction in phylogeny has two aspects, each of which has its equivalent in ontogeny. Of these the one which first comes to mind is racial death—the actual cessation of continuity with the blotting out of the line. The other is the transmuting of a given species into one of higher or more specialized type. The first is comparable to childless death, the second to the passing on of life to offspring. In each instance, except among the potentially immortal Protozoa, the individuals die but the line continues to exist.

Illustrations of the two methods of extinction may be found among the Miocene three-toed horses. Some, like the browsing "forest" horse, *Hypohippus* (see Chapter XXXVI), died without issue, due to increasing aridity of climate and the consequent shrinkage of their natural environment and food supply, together with the specialization of their teeth for succulent vegetation only. Another horse, contemporary with *Hypohippus*, was *Merychippus*, the blood of which, for aught we know to the contrary, flows in the veins of all existing horses, although *Merychippus as such* has ceased to be and may be reckoned as an extinct animal just as truly as *Hypohippus*.

In several instances among prehistoric forms extinctions have come with apparent suddenness so far as our records show, and in each instance without known competitors which could possibly

have worsted the race in an interracial strife. As the representatives of these forms often showed in one way or another certain of the phylogerontic characteristics which have been mentioned, the inference is that they died a natural death. Instances are the dinosaurs, of which the first to be rendered extinct were the gigantic Sauropoda, *Brontosaurus* and its kind, most of which died out long before the final extinction of the dinosaurs as a whole; and when the race had well-nigh run its course, we see some forms gigantic, others spinescent, others toothless, and the marvel is, not that they died, but that they survived so long, for the years of dinosaurian dominance exceeded one hundred and forty million!

Another group which seems to have died a natural death were the so-called "fish-lizards" or ichthyosaurs (see Fig. 55) which swarmed in the high seas of the Mesozoic almost from its beginning, but died out early in Upper Cretaceous time. Possible competitors were the mosasaurs or sea-lizards, whose known remains are confined to the Upper Cretaceous, but the ichthyosaurs were whale-like, not only in appearance but also in inferred habits, and were more numerous and widespread in their prime than were the mosasaurs. They certainly could not have been in competition with the whales, for a long interval separates the respective times of their existence during which, unless the mosasaurs filled the rôle, the seas were bereft of whale-like forms. The mosasaurs and plesiosaurs died abruptly without apparent cause at the close of the Mesozoic, as did the dinosaurs, and, like the latter, showed gigantic forms toward the close of their career.

Causes of Extinction

The causes of extinction (racial death) as applied to mammals have been admirably worked out by Professor Osborn (1906). As these laws probably cover nearly all extinction-causes in forms other than the mammals as well, they may be briefly summarized.

Changes in Physical Environment.—These are the changes wrought by the elevation or subsidence of land masses, with the resultant formation or severance of land-bridges, either facilitating or preventing migrations, or, by permitting incursions of hostile animals, producing competition which cannot be withstood. Restriction of habitat, especially insular habitat, also increases competition at the cost of the weaker forms. On the other hand, insular animals which do survive are isolated from further competition and

may live long after the general extinction of their kind elsewhere. Witness the monotremes of Australia and *Sphenodon* of New Zealand.

Changes in Climate.—Increasing cold is apparently a very potent cause for extinction, for while certain forms like the musk oxen and the Siberian mammoth may become adapted to rigorous climate, many more will fail. The last glacial period was a time of wholesale extinction, either as a direct or indirect result of the devastating cold.

Increase of moisture diminishes the supply of harsher grasses which afford nourishment to the great host of grazing mammals, and by far the great majority of hoofed animals extant are of this nature. Moisture also fosters the growth of poisonous plants and increases the numbers of insect pests and the consequent misery which they cause. The latter are often the carriers of disease such as the surra sickness and the sleeping sickness, which are fatal to domestic horses and, in the latter case, to men. Increase of moisture also gives rise to forest tracts which may form effective barriers to the migration of certain animals, and on the other hand afford migratory tracts to the semi-arboreal carnivores like the jaguar.

Decrease of moisture changes the character of the food supply, increases the length and severity of the dry seasons, removes forest barriers, thus increasing competition through the permitted migration of invading hordes, and actually causes the direct extinction of such forms as the primates, which depend upon forests for their livelihood. The extinction of primates in North America, with, and possibly as a result of, the increasing dryness toward the close of the Eocene is an historic fact. Diminution of the succulent herbage and increase of grasses, which are direct results of moisture diminution, favor the grazing but eliminate the browsing forms. An instance would be the extinction of the browsing titanotheres and forest horses and the great spread of grazing horses, camels, and other grass-feeding types in the Oligocene and Miocene epochs.

Changes in Living (Biotic) Environment.—Competition is inseparable from life, and while the adaptable forms are impelled thereby to rapid evolution, the inadaptable often find the competition too severe to be met and consequently perish. This competition may be brought about by one of two ways: by rapid multiplication of certain local or native animals, or by the immigration of new animals, giving rise to the slow or rapid extinction of certain local

forms. This may be due to direct competition, as when a mother marsupial is attacked by another animal; her young which she is forced to carry handicap her greatly in comparison with a placental mother, and her destruction means also that of her young. The food supply of larger forms may be destroyed by smaller grazing mammals. St. Helena, once heavily wooded, has been rendered a barren rocky island through the introduction of goats by the Portuguese in 1513, as they destroy the seedling trees and hence when the old ones died there were none to take their place. This must have had a profound effect upon the native forest-dwelling fauna.

Restrictions of *island life* result in the dwarfing of native forms through hard conditions and competition, as for example in the Shetland ponies, which are dwarfed far below the standard of their species. Certain islands in the Mediterranean, Cyprus, Malta, Sicily, and Sardinia, have yielded the remains of Pleistocene dwarf elephants, all of which are now extinct. These islands are relics of old migratory routes.

The *introduction of higher carnivorous mammals* often brings extinction to lower forms of a less well-equipped type. The entrance of the dingo, a placental dog presumably of Asiatic stock, may well have been the cause of the extinction of the native marsupial "wolf," *Thylacynus*, in Australia (see also page 124). *Thylacynus* is now confined to Tasmania whither the dingo has not yet penetrated, but its remains are found in superficial deposits in Australia, showing it to be only recently extinct. The migrations of the saber-tooth cats into South America during the Pliocene probably were a supplementary cause of extinction of the giant sloths, *Mylodon* and *Megatherium*.

Internal Causes.—Inadaptive structures such as the *highly specialized teeth* of browsing quadrupeds like the titanotheres, conformable only to the needs of a browsing form and incapable of supplying subsistence when the forests shrank and the grasses became dominant, may well have been an important factor in their sudden extinction. *Unprogressive feet*, such as those of the Amblypoda, archaic ungulates, could not bear their owners to the evolutionary goal when the competitors were the swift-footed forebears of modern hoofed animals. *Large size*, aside from its indication of racial senescence, is in itself a menace, as it requires more food for its sustenance and there go with it slow breeding and a

long period of adolescence which multiply the creature's chances for destruction before it can procreate its kind.

Extreme specialization always greatly increases the creature's risk, for the unspecialized frequently survive where the specialized, whose dominant organs may tend to over-development, perish.

Osborn gives four measures of *mental capacity* in extinct types: (1) absolute size and weight of brain, (2) convolutions, (3) proportionate size of frontal lobes or cerebrum, the seat of intellect, (4) ratio of brain to body weight. Among mammals especially a premium has been placed upon mentality ever since their initial evolution, and the shrewder of two competing groups generally wins. In the competition of dingo and thylacine mentioned above, relative mentality, which is notably deficient among marsupials, may well have been the deciding factor. In the old-time competition of archaic and modernized mammals (see Chapter XXXII) the former were handicapped by inadaptive feet, teeth, and brain, and the last count especially was the one upon which they stood condemned.

Osborn thus concludes: "Following the diminution in number which may arise from a chief or original cause, various other causes conspire or are cumulative in effect. From weakening its hold upon life at one point an animal is endangered at many other points."

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SECTION 2. MORPHOLOGY AND ADAPTATIONS

CHAPTER XV

COLORATION AND MIMICRY

Coloration

Everyone, whether a trained observer or not, has been struck with the wonderful range of colors borne by different members of the animal kingdom, and this is especially true in the tropics, where riotous color is the rule. In New England, on the other hand, conspicuous coloring is relatively rare.

To the student of biology, coloration of animals is of striking interest, for much of it is intelligible as part of the great adaptation scheme of nature; but all colors are not adaptive and sometimes it is apparently impossible to account for the existence of certain hues from the standpoint of utility. Our first question therefore is as to the means whereby color is produced, after which we may pass to a discussion of its significance.

Color Production

Color in nature is the result of some sort of interference with the beams of white light, either through the absorption of certain of the component rays, allowing others to be reflected to the eye, or by some arrangement of surface sculpturing or prismatic glass which refracts a beam of light and breaks it up into its constituent rays. The first method is chemical, by means of the absorptive powers of a definite pigment, melanin, the oxidation of which produces the various colors, and the second is physical.

Chemical Colors.—Pigment is found in nearly all portions of an animal's anatomy, not only on the surface but in the deeper-lying parts as well. In some instances the color is merely due to the absorptive powers of the chemical substance of which the tissues are composed, as for instance, the hæmoglobin, a compound of iron which gives the red color to the blood of the vertebrates and certain worms, or hæmocyanin, which gives the blue color to the

blood of the octopus. Both of these substances have a respiratory function, as they are the oxygen-carrying media of the blood, and their color is determined just as that of any mineral or chemical substance is determined and has no other significance to the animal in which it is found.

Again, the pigment may be external and give a color to the organism which may have a real value in the struggle for existence. Such pigment seems to be primarily for that purpose, and the cells which contain it are differentiated into plain pigment, which gives an unchanging hue to the animal, that is, one incapable of rapid temporary alteration, and chromatophores or changeable pigment spots, such as produce the flushes of color which pass over the skin of a chameleon or of a squid. These are cells which have radiating fibers lying in a plane parallel to the surface of the skin. During a period of relaxation the mass of pigment lies deep and thus presents but a small visible area; upon contraction of the fibers, however, the pigment is spread over a greater portion of the surface and thus is manifest to the eye. Two sets of contrastingly colored chromatophores, such as brown and green, expanding alternately, change the general hue of the animal from brown to green or the reverse as the case may be. The chromatophores, influenced by the eyes and skin through the pituitary gland, produce color changes, as for instance in the African chameleons or the American lizard, *Anolis*, the false chameleon of the southern states. The effect of these chromatophores is greatly enhanced when there lies beneath them a reflecting layer formed of guanin, a substance allied to uric acid. This mechanism is particularly effective among fishes.

Physical Colors.—Another change or play of colors is caused by surface structure, light falling upon which is reflected by finely incised parallel lines, often running in more than one direction, and thus undergoing dispersion into its component rays. The latter device is comparable to that used by physicists for spectrum analysis, and known as the Rowland grating. This instrument is generally made of spectrum metal which does not readily tarnish, upon which are ruled, with an engine of highest precision, some ten to twenty or even forty thousand parallel lines to the inch. A beam of light falling upon such a grating is broken up into its component colors, giving the rainbow effect known as the spectrum and comparable to that produced by the passage of the beam

through a crystal prism. The sculptured surface of a beetle's wing or the scales upon that of a butterfly or the feathers of a humming-bird's throat produce the same result, except that instead of a series of colors such as those of the rainbow, but one may usually be seen from a given point, and this changes to another when the angle of vision is changed. The tropical butterfly *Morpho* ranges from blue to a greenish hue, while the ruby-throated humming-bird or the neck of some pigeons changes from a brilliant metallic red to a lustrous green. The scales of *Morpho* when seen under the microscope exhibit two sets of striæ perpendicular to each other, which accounts for the play of single colors rather than a spectrum, due to their mutual interference. Strangely enough, the actual color of the scales as seen by transmitted rather than reflected light is neither green nor blue, but brown.

Biological Significance of Color

Indifferent Colors.—From the biological standpoint, the colors of animals may be considered under various heads. Of non-selection value but possibly of vital importance to certain ancestors of different environment are certain so-called "indifferent colors." Of such would be the brilliant scarlet of some of the filaments or fin-rays or body of certain deep-sea fishes. These colors are borne by heredity, and as they are not detrimental, being invisible in the Stygian darkness of the deep sea, they are not eliminated. Colors or markings such as the spots on the uniformly black fur of a melanic leopard (see below), or those sometimes seen in the coat of a domestic horse are further illustrations.

Albinism is total absence of color in hair, feathers, or skin, and even in the iris of the eye. The latter permits the color of the blood to show, causing the pink eyes so characteristic of pure albinos. The hair and feathers are white because the tiny spaces which normally should be filled with pigment granules are full of air, which reflects all of the light rays just as froth or sea-foam does.

Melanism is the reverse of albinism, for instead of absence of pigment in the skin there is a profusion of black melanin, giving a totally black hue to the entire animal. In both albinism and melanism color markings may be plainly visible, but in the same manner that the pattern shows in a piece of brocade or damask fabric. An albino peacock, for instance, whose feathers are en-

tirely white, shows the eye-like markings so characteristic of the tail plumes of the normal bird, and the black leopard, as has been said, shows the spots in the same way.

Both albinos and melanos often arise as sports or saltations in a brood or litter of normally colored individuals. That they are germinal variations is evident, for not only are they heritable mutations but they follow Mendel's law in the ratio of their appearance. Certain races of albino birds and mammals have been established among domestic forms, such as white mice, rabbits, chickens, and pigeons, while the silver fox is a melanic phase of the common red fox, *Vulpes fulvus,* which, though occurring sporadically among wild broods, is now a well-established and commercially profitable domestic variety, of which there are several distinct strains. In nature these sports should be distinguished from normally white or black species such as the various white species which inhabit the snowclad Arctic regions. Lack of pigment shows every degree of gradation from pure white through blotched or piebald individuals to those which show but faint traces of white.

Valuable colors are such as evidently serve a direct physiological need. They have been classified under the following heads according to the uses to which they are put:

- Sympathetic colors
  - Protective, of the hunted
  - Aggressive, of the hunter
- Alluring colors (see under aggressive mimicry, page 212)
- Warning colors
- Mimetic colors
- Signal and recognition marks
- Confusing colors
- Sexual colors

Sympathetic, cryptic, or concealing coloration is that wherein the hue of the animal harmonizes with its surroundings in such a way that it blends into the background and loses its conspicuousness in order to escape from its enemies or to lie in wait for its prey, as the case may be. To the first, the name protective coloration is applied, as in the case of an Arctic hare, while the second group may be called aggressively colored, the Arctic fox being an example. In the final analysis, however, both are protective, as it is

just as essential to the fox that he be protected against starvation as it is to the hare that *he* be protected against slaughter.

The same species may vary in color in two ways, known respectively as *local colors* and *seasonal colors*. In the first the species has a wide range over areas varying in general hue, so that the ground color of the animal, if sympathetic, must also vary to harmonize. Several grasshoppers (Acrididæ) whose hind wings are brilliantly colored red or yellow have the fore wings (beneath which the hinder ones fold when at rest), as well as the remainder of the body, colored to harmonize with the earth. Those found upon the area of the red shale in New Jersey, for instance, will have reddish brown fore wings, while the same species near the sea-shore will be light gray to harmonize with the prevailing sands. The gazelle, one of the most wonderful instances of desert adaptation, varies from white on the great sand plains to dark gray on the lava fields of volcanic districts. Among the hawk-moths the caterpillar of that found on the convolvulus (*Sphinx convolvuli*) when full grown is either green like its food-plant or brown like the ground beneath. It thus shows a double adaptation, each phase of which is apparently capable of protecting it to the same extent; as a matter of fact, however, the brown color is more effective than the green, as we may learn from two facts. In the first place, the four young stages of the caterpillar are green, and it only becomes brown in the last stage, though sometimes even then it remains green. This suggests that the brown is a relatively modern adaptation, and probably would not have arisen had it not been better than the original green. In the second place, the green-colored caterpillars are much less numerous at present than the brown ones, and this implies that the latter survive oftener in the struggle for existence (Weismann).

Another still more remarkable case is that of the æsop-prawn, *Hippolyte*, described by Gamble: "The wakeful hours of Hippolyte are hours of expansion. The red and yellow pigments flow out in myriads of stars or pigment cells [chromatophores]: and according to the nature of the background, so is the mixture of the pigments compounded to form a close reproduction both of its color and its pattern: brown on brown weed, green on Ulva or seagrass, red on the red Algæ, speckled on the filmy ones. A sweep of the shrimp net detaches a battalion of these sleeping prawns, and if we turn the motley into a dish and give a choice of sea-weed, each variety

after its kind will select the one with which it agrees in color, and vanish. At nightfall, *Hippolyte*, of whatever color, changes to a transparent azure blue: its stolidity gives place to a nervous restlessness; at the least tremor it leaps violently and often swims actively from one food-plant to another. This blue fit lasts till daybreak, and is then succeeded by the prawn's diurnal tint. Thus the color of an animal may express a nervous rhythm."

A number of birds and mammals such as the ptarmigan, the Arctic fox, the varying hare, and the weasel which puts on royal ermine for its winter dress, show a change of color from summer to winter, harmonizing with the browns of leafy soil or rock in summer and with the snow-covered ground in winter. The immediate stimulus to change on the part of the individual may well be increasing warmth or cold as the case may be, but temperature change is not believed to be the *direct* cause of the original assumption of the adaptation, for the common European hare, *Lepus timidus*, does not change its coat in spite of the cold. On the other hand, the varying hare, *Lepus variabilis*, also remains brown throughout the winter in southern Sweden, although the weather there may be exceedingly cold. In the higher Alps the same species remains white for six or seven months, in the south of Norway for nine months, and in northern Greenland it is always white, as the snow rarely melts, except in localized areas, even in summer. The lemmings also turn white in winter but experiments have shown that a captive lemming kept in a room in winter will not change color until exposed to the cold, the cold acting as a stimulus which incites the skin to the production of white hairs.

Standard Faunal Colors.—It has been found that each of the several different life conditions under which animals are found is apt to make its impression upon its denizens in certain definite ways so that their habitat is usually readily inferable from their general appearance, and this is notably true of color. For example, the desert animals are generally duns or grays such as the gazelle already referred to, the camel, and the lion. Plains-dwelling forms are wont to simulate the color of dry grass, as in the case of the familiar "buckskin" horses which become invisible at distances at which black, bay, or white horses are readily seen. Jungle folk are often striped like the tiger or zebra, highly conspicuous forms when viewed in the menageries, but with colors which simulate the bars of sunlight and the lights and shadows

among the tall jungle grasses. In the open, on the other hand, Roosevelt tells us that a little distance away the zebra's stripes become indistinct and he appears a uniform gray (see page 206). Forest-dwelling forms are usually dappled, giving the effect of the splashes of sunshine caused by the pencils of light which fall through the interstices of the leaves. Instances are the leopard and jaguar, the fallow deer, the boa among serpents—although here the pattern is more definite but wonderfully harmonious. Some forms like the Virginia deer, the tapir, and the lion are spotted when young but more uniformly colored when adult, which may well be of ancestral significance. Many forest insects are green, simulating the chlorophyl of the leaves very closely. Birds of temperate climates are rarely so, but in the perpetually green forests of the tropics green birds of many different and unrelated families are abundant. Green insects hibernate, generally in the egg state, during the sere months in northern lands, but green birds, unless they be migrants, would be highly conspicuous when the trees are leafless.

Arctic creatures are as a rule white, except the aquatic forms like the seals and walrus, and certain of these (*Phoca* spp.) are white when very young. But if a polar bear were brown or black he would inevitably starve, and on the other hand, a white animal away from the snow fields would be equally hard put to it to make a living.

Sea and air mark their inhabitants alike, that is, if they are aggressive or wandering forms. Many sea birds are steely gray or blue above and white beneath, which makes them harmonize more or less with the sea when viewed from above and with the sky when seen from below. Among the forms thus colored are the gulls and terns. Many fishes such as the blue-fish and mackerel are similarly colored and for like reasons, even though they are aquatic rather than aërial. One curious instance is cited of a pelagic snail, *Glaucus*, which floats belly upward on the surface of the sea. Here the colors—blue on the ventral and silver-white on the dorsal side—are reversed with reference to the snail's anatomy, but normal from the standpoint of its life habits.

Nocturnal creatures also wear a proper uniform of mottled brown or gray such as one sees in the wild-cat or owl, which renders their prowling owner very difficult of discernment in the dim light, even to those with night-adapted vision.

Warning or revealing colors are the conspicuous reds and yellows such as one sees upon the bodies of poisonous or unpalatable animals like the hornet, coral snake, tiger salamander, Gila monster, and many caterpillars and butterflies. These creatures are practically immune from attack if they are recognized in time, so that the advertisement of their dangerous nature must be a very conspicuous one. It does not profit a nauseous butterfly if it is not eaten after it is killed, it is the killing that must be avoided, and a single stroke of a bird's beak might well be sufficient to render the butterfly *hors de combat.* Its character must be recognized at once before the chance of fatal injury occurs. It may be that a few fatalities on the part of the butterflies are necessary in order to impress each individual bird; on the other hand, the inherited instinct may warn the bird that conspicuously colored animals are to be left alone, or tradition may take the place of instinct. At all events, most preying animals do recognize and avoid the warningly colored forms within the scope of their natural environment, but may have to learn by bitter experience to avoid strange enemies. Experiments go to show that when hungry animals have been duped once or twice by having conspicuously colored unpalatable caterpillars offered to them, they learn to discriminate and the coloring aids very largely in the attainment of this lesson. This is true even of the relatively unintelligent fishes.

While the warning coloration may well be the result of natural selection, it has been suggested that very abundant deposition of a waste-matter pigment may render an animal at once unpalatable *and* conspicuous. This, however, would not account for the mimetic coloring to be discussed later (see page 211) which renders a *palatable* insect conspicuous and therefore immune from attack, nor does it seem sufficient to account for the development of warning coloration in edible forms endowed with weapons of defense.

Warning coloration sometimes carries with it the assumption of an attitude which heightens the effect and may be designed to strike terror to the enemy's heart. Such for instance is the spreading of the "hood" of the spectacled cobra (cobra-de-capello) in which the flattening out of the ribs of the neck region displays the conspicuous markings upon its dorsal side to advantage. A small moth, *Smerinthus*, has large eye-like spots on the hinder wings which are concealed by the forward pair when the insect is at rest; when it is annoyed, however, the wings are raised in such a way

that the great, staring, eye-like markings are displayed, an exhibition which must greatly impress the would-be assailant.

Mimetic coloration will be discussed at greater length later in this chapter (pages 208–212). In brief, it is a color resemblance between an animal and any other object, animate or inanimate. It may be either such as to conceal or it may be a warning coloration, but in the latter instance it is merely a "bluff" though nevertheless of highly effective defensive value.

Signal marks are apparently of very great importance among gregarious animals where mutual aid in time of danger is a characteristic. A herd of Virginia deer may be quietly grazing when one of the number becomes aware of danger. As he starts off, up goes the tail like a signal flag, showing the conspicuous white of the under side and the adjacent parts of the animal's body which the lowered tail had covered. This acts as a warning to the others and in an instant the herd is in full retreat. The American antelope (*Antilocapra*) has conspicuous areas of white hair on either rump which can be flashed in a similar manner through a spreading of the hair which reflects more light and forms a very effective danger signal. A still more familiar example is that of the cottontail rabbit, *Lepus sylvaticus*, whose signal flag gleams in the dusk and shows its young the way to safety. In each instance the signal is instantaneous, which may be of vital importance to the safety of the individuals.

Recognition marks, for use of other individuals of the same species, are such as the red and orange spots on the side of a brook trout (*Salvelinus fontinalis*) which render it so beautiful a fish. In general the trout obeys the law of sympathetic coloring, a lurking fish in a shadowy pool being almost invisible to the enemy above, as his dusky back is as harmonizing from that point of view as his light-colored belly would be from below; but to creatures of his own kind and at his own level the characteristic speckledness is clearly discernible. These recognition marks are also borne by many insects and are often, as in many butterflies and moths, visible only when the animal is in motion, for then no amount of protective coloration will generally avail its owner. Under such circumstances the sympathetic colors are on the exposed portions of the animal as it rests with wings folded, that is, on the upper surface of the fore wings in moths and the under surface of both pairs in butterflies, for in the former group the hind wings are

folded beneath the fore, which lie roof-like against the sides of the body, while the butterflies bring the upper surfaces of the erectly held wings together, thus exposing their under surface.

Confusing Coloration.—With many forms such as the moths and butterflies which we have just described, the recognition coloring may be very conspicuous, so that during flight, when no protective coloring would avail, the eye follows it readily. A sudden settling of the insect, the brilliant color instantly disappears, and one loses sight of the insect completely, since its exposed coloring now harmonizes with the support on which it rests. Were the eye to follow the sympathetic color during flight, the resting insect would be much more readily discerned, but the sudden disappearance of the conspicuous color is highly confusing to a human observer, who looks in vain for the colored object and overlooks it in its transformed state, and the same must be true of pursuing creatures as well. The Catocala moth, with red-banded hind wings, is an instance in point, and this coloration is not at all confined to insects, as certain somber-colored lizards have brilliant color on the under side of the tail, which the eye follows and loses as the creature stops after one of its lightning runs and, lowering the tail, crouches in the sand, with which it now harmonizes to perfection.

Sexual Coloration.—As we learned in the chapter on sexual selection, the males of birds and other forms are often much more conspicuously colored than their females, as for instance, the cardinal bird with his gorgeous red nuptial plumage as compared with his soberly garbed mate. Other similar contrasts are seen in the oriole, bobolink, several ducks such as the wood duck and the eider, in the wild progenitor of domestic fowls, and in the related pheasants. Why the males are conspicuous is perhaps not so clear, but the protective coloration of the female must be of prime importance to the race, especially if she is nesting or a potential mother. The young males which have not yet reached sexual maturity are also protectively colored, so that in many cases it is extremely difficult except through anatomical examination to distinguish the young male from the female bird, even though the color contrast is so marked in the fully adult. The brilliant color of the cardinal bird is gradually assumed, several years being required for its perfection.

The spotted coat of young animals, such as the deer, lion, and

puma, is well known. The young Brazilian tapir is somewhat irregularly striped, which is also true of the young of the wild boar. The jungle fowl, the ancestral stock of our domestic chickens, are colored in their adult life much like the game cock. The newly hatched chicks, on the other hand, instead of being plain yellow or dark-colored as in most domestic breeds, bear two dark longitudinal stripes along the back. That all of these infantile colors are of superior protective value to those of the adult, especially under the conditions surrounding babyhood, is, in many instances, evident, but some may well be more of historic than of immediate significance.

In a higher insect such as a moth or butterfly, egg, larva, pupa, and adult may each have a protective coloration suited to the immediate environmental need and differing markedly in each successive stage. That these colors aid in increasing the percentage of survival in each of the several stages is evident.

Biological Cause of Coloration

Some coloration is doubtless dependent upon the chemical material of which any organism is composed and the hue is due entirely to the absorptive powers of that substance; since oxide of iron is red, so is the blood of vertebrates, and since copper oxide is bluish green, so is the blood of the octopus, and so on. In many cases the color of internal organs may be due entirely to the nature of the food consumed; thus the flesh of brook trout caught in central Massachusetts where there are few crustaceans available for food is pale, whereas trout from the Adirondack lakes where crawfish are abundant have flesh of a deep salmon pink. The bones of a gar-pike are green in color through the deposition of green vivianite under certain physiological conditions. Thomson says that "the pigment substances are primarily waste-products, reserve-products, or by-products of the animal's metabolism, and in many instances the colors have no more significance for their possessors than the gorgeous autumnal tints of withering leaves have for the tree—that is to say, none!"

Pigment, aside from its protective or warning significance, may have other very real values. Such for instance are the definitely localized spots of coloring matter which are sometimes associated with end organs of the nervous system. This pigment absorbs light, indirectly stimulating the nerve, and thus acts as a light-

percipient organ. All eyes have this for their basic principle, but in some instances accessory organs which are not strictly speaking eyes and yet have a light-perceptive value are thus formed.

Other pigments found in fur or feathers may serve to absorb or reflect heat and thus be of value to the owner in addition to the function of sympathetic coloration, such for example as the pale grays of the denizens of the desert. Again, dark pigment such as that in the negro and other dark human races serves to cut off the ultraviolet rays of light which from their physiological action cause such discomfort to humanity. Hence a colored man under a tropic sky is less liable to sunstroke than a fair one, and the development of human pigment, which is said to bear a direct ratio to the number of sunny days in a year in a given region, may well be due to the working of natural selection in eliminating the lighter colored individuals rather than to the inheritance of the direct effect of the sun's rays in the production of pigment.

The structural features, striæ and the like, which give rise to the physical play of iridescence, have been compared to ripple-marks or rhythms of growth such as the growth-lines on a shell, and the same may be true of the color when it is laid down in concentric lines or cross-bars.

Value of Coloration

The value of coloration to the animal is in many instances a very real thing and must play an important part in determining the creature's chances for survival. That it is not in every case operative, however, is undeniable, for, as Roosevelt says, speaking especially of the higher animals, some have so wide a range of activity, continually passing over such totally different landscapes and among such totally different surroundings, that the difficulty of devising a concealing coloration would be enormous (1911). Perhaps one of the most glaringly conspicuous of animals as seen in the zoölogical parks is the zebra. The question arises as to the value of this coloration, either as concealing color or as recognition marks. Gregory has summarized the evidence as follows: "Pocock maintains with much force that the testimony of observers in the field has established the truth that the coloration of the coat renders a zebra invisible under three conditions, namely, at a distance in the open plain at midday, at close quarters in the dusk and on moonlight nights, and in the cover afforded by thickets."

On the other hand, the late E. C. Selous, a keen observer with a lifetime of field experience, writes in *Great and Small Game of Africa*: "Never in my life have I seen the sun shining on zebras in such a way as to cause them to become invisible or even in any way inconspicuous on an open plain, and I have seen thousands upon thousands of Burchell's zebras." He admitted the fact that the bold black and white stripes on the coat of Burchell's zebras are not apparent at any great distance but stated that nevertheless the zebras, on account of their constant movements and by the violent switching of the tail, were always conspicuous even in the moonlight. Moreover, the lions hunt the zebras chiefly by smell and at night, or lie in wait for them at the water holes. Colonel Roosevelt also vigorously supported the view that the striping was of no special use for concealment.

With reference to the value of the stripes as recognition marks, Selous thought them of little service, but Ewart, in his famous Penycuik experiments in which a male zebra was mated with an Arab mare, had great difficulty in overcoming the reluctance of the zebra, for only after he had become accustomed to the strange appearance of the dark-colored, unstriped mare could he be induced to mate with her at all. Zebras are such keen-eyed animals that they can hardly fail to recognize individual, much less specific, differences in their companions.

Nevertheless, if the color was such as to protect the bird or animal at critical periods, not only from the standpoint of its own individual protection, but also from that of the race, as for instance during the bringing forth of the young or the incubation of the eggs, its value would be abundantly proved even though at other times the protection afforded was inadequate.

Whatever may be the initial cause of color, its final perfection of adaptation for concealment, warning, or whatsoever service it may render may well be the result of the natural selection factor.

Mimicry

Of all the devices adopted by nature for the protection of her children none is so marvellous in its perfection as those which are included under the head of mimicry—the resemblances which organisms bear to others and to inanimate objects in form, color, attitude, and action, thereby either escaping observation or advertising an apparent harmfulness which is not at all real.

Just as coloration of animals was classed as protective and aggressive, so we may consider two aspects of mimicry, the protective mimicry being as before divisible into concealing and warning and the aggressive into concealing and alluring. Mimicry may be further divided into unconscious or passive, under which head by far the greater number of mimics fall, and in which form and color make up the resemblance; and conscious or active, in which by its actions as well the mimic imitates the immune model.

Almost anything may be mimicked, from a wave-worn pebble to a twig of a tree or an active harmful insect. Thus all the kingdoms of nature, the inorganic, plant, and animal, furnish the host of models to be imitated where immunity is sought.

Protective mimicry, as we have seen, has two aspects, concealment and warning, of which the first is by far the more common. An example is the crab *Cryptolithodes* whose smooth rounded form and texture and white color harmonize so perfectly with the white quartz pebbles of the beach that one needs must turn the animal over, generally by accident, to see its real organic character as a living form. The immunity which it thus secures from enemies of its own humble station must be of real protection, though doubtless it is occasionally crushed by a larger form. Its mimicry is certainly unconscious, as action betrays its presence and stoical passivity is essential to safety. Another crab resembles wave-worn dead coral very closely; here, as the animal is carnivorous, the concealment may have a twofold purpose, protection against its enemies and aid in securing its prey.

The geometrid moths, whose caterpillars (see Fig. 25) are the familiar measuring worms, are often not only protectively colored but may mimic the twigs and smaller branches of various plants such as clematis, the birch tree, the pear tree, and many others. That on the birch, the caterpillar of *Selenia tetralunaria*, when it needs particularly to escape observation, grasps the branch with its two hinder pair of prop-legs and throws its body outward at an angle, in a rigid posture as though in a cataleptic state. Details of resemblance are now apparent, not only in color and form but in excrescences which simulate the latent buds of a twig, while the somewhat pointed head and feet resemble terminal buds. So perfect is the resemblance and so long maintained the posture that even a trained observer often fails to see the creature or to be sure of what he sees until he actually touches it. Such mimicry

is in the main unconscious, that is, in the color and form, but as action precedes the inaction of the mimicking pose it is also in part a conscious one.

Yet another geometrid moth, *Schizura mucronis*, carries the mimicry still further, for not only does the rough-barked caterpillar mimic the twig to perfection, but the moth does also, although somewhat less effectively. The latter rests head downward against the bark of the actual limb with the stiffened body held out at an appropriate angle, the wings being folded around the abdomen in such a way as to heighten the resemblance.

Many moths mimic the rough bark in color when in an ordinary resting posture upon it, but with them it is a matter of color mimicry only.

Many of the walking-stick insects (Phasmidæ) are also close mimics, with their slender body, attenuated limbs, sympathetic coloration, and slow movement, often stiffening into rigidity as do the geometrids. When moving, some of the walking-sticks have a peculiar tottering gait, but in one instance in Texas, while the shadow of the insect could be clearly seen upon the shadow of a bush because of this characteristic, only careful search revealed the creature in substance upon the bush itself. All of the American species of phasmids are wingless and there are comparatively few of them, but in the tropic and subtropic regions of the earth over six hundred species are known, many of which have other protective resemblances, some of them marvellous indeed. Perhaps the most perfect example is the leaf insect *Phyllium* (Fig. 29). Here the wings and flattened and expanded body and limbs are all green except for irregular small yellowish spots which simulate the fungus or rust growths upon a leaf so that the total resemblance is very precise.

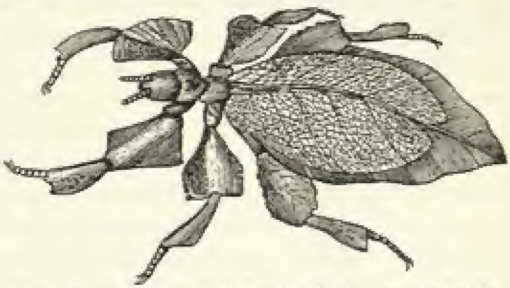

FIG. 29.—*Phyllium*, "walking leaf," an example of insect mimicry. (After Doflein.)

Many butterflies are also leaf-like in appearance, simulating not only the general hue of a dead or withered leaf but its petiole,

midrib, venation, rust spots, and the clear places which sometimes occur in a diseased or injured leaf. One such butterfly is *Cœnophlebia archidona* from Bolivia, in which the upper outer angle of the fore wing forms the apparent stem or petiole of the leaf; the most noteworthy instance, however, is that of *Kallima paralecta* from India (Fig. 30) in which the hinder wings are prolonged into the stem-like structure, and the other leaf-like markings are carried to an extreme of perfection. This butterfly is strikingly colored above, blue-black with a reddish yellow or bluish white band, the recognition markings of the species. This coloring is seen in flight. On the instant of alighting, the insect practically disappears, for now the wings are folded together so that only their protectively colored under surface is exposed. This is deceptively like a dead and sere leaf due to its color, in which red and brown alternate with occasional spots bereft of scales which simulate dewdrops. In addition there is seen the midrib and often the lateral ribs of the leaf, and black and mouldy spots also occur.

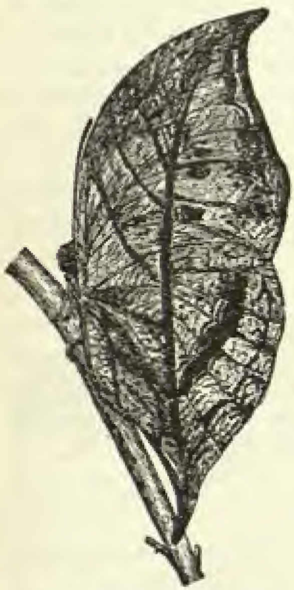

FIG. 30.—Dead-leaf butterfly, *Kallima paralecta*, from India. (After Weismann.)

Warning Mimicry. — Some of the most remarkable mimicry of all is included under the caption of warning mimicry—mimicry of advertisingly colored forms which are distasteful or even poisonous either when devoured or through the possession of poisonous fangs. Among reptiles there are certain brilliantly colored poisonous snakes belonging to the same family (Elapidæ) as the deadly cobras. These snakes are of the genus *Elaps* and are confined entirely to America. They are beautifully colored, often in red and black alternating bands which in the coral snake are edged with yellow. While they possess a strong poison they are practically harmless to man because of the limited extent of the gape. Each of the several species of poisonous coral snakes is mimicked by other species of harmless snakes belonging to different genera, and while the markings are in no case exactly similar, the approxi-

mation is sufficiently close to render the imitators practically immune from attack except perhaps by mankind. Many other harmless snakes such as the hog-nose snake (*Heterodon*), while not colored exactly like poisonous ones, will nevertheless flatten the head, rendering it triangular, and hiss and often strike to show how very dangerous they are. With lower animals this doubtless gives them a certain immunity from attack but on the other hand only serves to invite destruction at the hand of man. The mimicry in those species which imitate the coral snakes is unconscious or passive, that of *Heterodon* is conscious as it depends upon the actions of the snake to make it effective.

Among insects again there are a host of imitators, both active and passive; those which mimic their models in form, color and action, such as the hairy, brilliantly colored syrphus- or flower-flies which resemble the stinging bees and wasps; beetles which resemble wasps; clear-wing moths which mimic bees, and so on. Some of the most remarkable imitations, again, are among the butterflies, which resemble other distasteful and hence immune butterflies. The most familiar instance is that of the immune monarch butterfly, *Anosia plexippus* (=*Danais archippus*), which is inedible, and its imitator, the viceroy, *Basilarchia archippus* (=*Limenitis disippus*), which would otherwise be destroyed, as it is palatable from the point of view of insectivorous birds.

Sometimes only the female of a butterfly will mimic an immune model, the male being colored in a totally different way (dimorphic species). Again in widespread species more than one form of female will be associated with a given male, each female mimicking an immune species which happens to be locally abundant. In Africa the Danaid butterflies are unpalatable, while the Papilios are not. *Papilio merope* is a species which has scarcely varied at all in the male sex in the extent of its distribution through Africa, but in the female has almost everywhere lost the outward appearance of a *Papilio*, and assumed that of a Danaid, which is protected by being unpalatable; and not everywhere the appearance of the same species, but in each place that of the prevailing one, and sometimes of several in one region. As a result, these females now show a polymorphism consisting of four chief mimetic forms, plus the primitive form—that resembling the male. The latter has survived in Abyssinia alone, and even there it is not the only one, but occurs along with some of the mimetic forms (Weismann).

Thus while in a general way the different types of female are locally separate, their areas of distribution often overlap, and, at the Cape for instance, one male and three forms of female have been reared from one set of eggs.

Aggressive mimicry is that shown by certain carnivorous forms such as the spiders found on golden-rod and other flowers, whose yellow bodies so harmonize with the flowers upon which they rest as to render them invisible to the visiting insects which form the spider's prey. Other spiders resemble oak galls or other vegetable growths, yet others the droppings of birds, all of which resemblances have the same ulterior design. These are all instances of concealing mimicry.

Another spider is described as resembling an orchid blossom more or less closely, both in color and form. In this instance the resemblance is an alluring one and is advertising rather than sympathetic. It is doubtless a highly profitable adaptation to the spider. Another similar adaptation is that shown in a certain African lizard, protectively colored except for a brilliant patch of color at the corner of the mouth which acts as a lure for the unwary.

Simulation of Death.—But one aspect of mimicry remains to be discussed, again a conscious imitation, that of simulating death. This has been developed to such an extent in the American opossum (*Didelphis virginiana*) that the act is known in common speech as "playing 'possum." Whether it is an intentional performance on the part of the creature, or whether, as has been suggested, the animal faints away from fright, in which event it could hardly be called conscious mimicry, it certainly is again an adaptation of real value to its owner and may often save its life when attacked by an enemy that prefers to kill its prey. Many insects, especially hard-bodied beetles, which a fall will not injure, have a similar habit, as they drop like a pebble when one is about to seize them, lie inert where they fall, and are often searched for in vain among the leaves and grass beneath the bush upon which they were. This may be, as in the case of the opossum, an actual unconsciousness, but is even more efficacious, as the animals are so hard to find.

Wallace's Conditions for Protective Mimicry.—Wallace long ago summed up the conditions which must be fulfilled whenever protective mimicry occurs. They are as follows:

1. Imitative species must occur in the same area and occupy the same station as the mimicked.

2. The imitators are always the more defenseless.

3. The imitators are always less numerous in individuals.

4. The imitators differ from the bulk of their allies.

5. The imitation, however minute, is external and visible only, never extending to internal characters or to such as do not affect the external appearance.

Causes of Mimicry.—Weismann, the leader of the Darwinian school, makes natural selection the only factor in the production of mimicry, arguing with Bates that the great likeness, such as occurs between the white butterflies and the nauseous Heliconiidæ, would depend on a process of selection, based on the fact that, in each generation, those individuals would on the average survive for reproduction which were a little more like the model than the rest, and thus the resemblance, doubtless slight to begin with, would gradually reach its present degree of perfection. In opposition to this it has been argued that the mimicry, to be of any selection value, must be practically perfect at once, and the minute or trivial variations such as the exponents of natural selection postulate would be of no possible survival value in mimicry. On the other hand, that masterpiece of mimicry, *Kallima* (see Fig. 30), goes too far, as a much less perfect imitation would be ample for all practical purposes and we can not conceive of selection taking an adaptation past the point of efficiency.

Another explanation of mimicry is that the mimetic form as in butterflies may have arisen as a large mutation, and that for a while the two forms persisted side by side, but gradually the old one disappeared. Such an explanation might well account for the polymorphism of *Papilio merope*, especially as the male still retains its original form and in one locality (Abyssinia) a female does as well.

There is little doubt, however, that whatever causes may be secondarily operative in the production of coloration and mimicry, natural selection is the chief.

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CHAPTER XVI

ANIMAL ASSOCIATIONS. COMMUNALISM

Perhaps one of the most interesting aspects of evolution is the development of communal life among animals, for here is foreshadowed one of the factors which have aided so largely in placing man at the head of the animal kingdom. It is not alone his sentient power and his hand skill that have made him great, for while individual man working his way as a solitary being can accomplish much, civilization and its attendant train of invention and attainment are the direct outgrowth of communal life.

Animal associations may be divided into several sorts, some of which have already been discussed. They are:

- Associations of different species.
  - Mutually beneficial.
    - Commensal (see Chapter II).
    - Symbiotic (see Chapter II).
  - Harmful to host.
    - Parasitism (see Chapter XVII).
- Associations of the same species.
  - Gregarious animals.
    - Mutual aid with no division of labor other than leadership.
  - Communal animals.
    - Always implying division of labor and sometimes physical differentiation.

Gregarious Animals

The association of unlike forms will not now be discussed and we may turn at once to gregarious animals. These are such as herd together for mutual aid, either for defense or for the securing of food. The name might also be applied to communities of sedentary benthonic animals whose association is the result of the accidental settling of a swarm of mero-planktonic young in a given locality. Such a group should not be called a colony, for colonial organisms, as the term is used in biology, are such as are organically connected with one another.

Truly gregarious forms are the shoals or schools of invertebrates or fishes such as the squid, shad, cod, mackerel, herring, and albicore. Whether there is here a recognized leader we have no means of knowing. Of higher forms among marine types there are the whales and seals, all of which are gregarious. With the killer whales, *Orcinus* (Fig. 57), there is mutual aid just as there is among wolves, for the purpose of destroying their prey, the killers being the only cetaceans which prey habitually on warm-blooded animals. Their victims may be seals, penguins, or the various species of their own order. The killers destroy such as they are able alone, but combine into packs when a larger whale is to be attacked. Their favorite food is the tongue of the right or whalebone whale, and two or three will seize the lips and force open the mouth, while the others tear out the tongue of the unfortunate victim.

Wolves, when they run in packs in the pursuit of prey, may be said to observe a sort of armed truce, the idea of mutual aid for defense evidently being foreign to their code of ethics, for they will at once turn upon, destroy, and devour one of their own band who happens to be wounded, even though it delay the chase. Ungulates, on the other hand, herd together for safety, not for food-getting, since the immense numbers sometimes brought together must render the amount of food available for an individual materially less.

Perhaps the greatest numbers of any large animal of recent times were those of the buffalo *Bison americanus* which formerly spread over one-third of the entire continent of North America.

Hornaday tells us that they ranged from the arid plains to the hilly hardwood forests of the Appalachians, covering an area which stretched 3600 miles from north to south by 2000 miles from east to west. The center of their abundance lay in the great plains from the Rocky Mountains to the Mississippi, and when the herds assembled there they covered the earth seemingly as with one vast brown buffalo-robe. One of the most memorable observations of the immensity of their numbers was that of Colonel R. I. Dodge in May, 1871, who drove for twenty-five hours through an unbroken herd of buffalo. Hornaday believes that Colonel Dodge must actually have seen no fewer than half a million animals. They belonged to the great southern herd, estimated at 3,500,000, then on its annual spring migration northward. The estimated numbers of the northern herd have been put at 1,500,000 making a total of 5,000,000 animals, and yet within the next four years that majestic army was reduced to three pitiful remnants owing to the wanton destruction by man, a slaughter second only to that of the World Wars. In 1903 Doctor Frank Baker estimated the

total number alive as 634 wild and 1119 in captivity, making 1753 as compared with their former millions. Since that time, the number has been so increased by wise conservation that the herds have to be thinned out from time to time, owing to limited grazing area.

Among buffalo, the herd is led by a female, while among horses, as is the case with the pariah dogs of Istamboul, a male of proved prowess is chief among the pack until displaced by a stronger.

Beaver carry their social organization further in that all unite for the construction of such public works as the dam which impounds the water. When it comes to the individual lodges, however, each works for himself and lives his own family life more or less independent of others of the community.

Among pelicans, even though they flock together in great numbers for breeding and the rearing of their young, each jealously guards its own interests and those of its offspring, regardless of the others. Occasionally, however, mutual aid becomes necessary, as when individual fishing is not sufficiently productive. In this event, the birds are said to swim in a line in such a way as to surround a school of fishes much as they are enclosed in a seine. The pelicans then swim toward the shore, driving their prey into shallow water, where each fishes for himself.

Some instances are recorded of the association of more than one species of gregarious animals. Colonel Roosevelt speaks of a herd of between forty and fifty elephants, accompanied by over a hundred white herons. In order to see whether there was an available bull among them, the men moved them by shouting, and off the elephants went at a rapid pace, half the herons riding on them while the others hovered alongside, like a white cloud. Another example is the association of zebra, ostrich, and gnu, mentioned before (see page 28) under the head of commensalism, as such associations of unlike forms for mutual good belong to that category. Roosevelt also tells us of oryx herds, generally of from half a dozen to fifty individuals, often mixed with the zebras. There were also solitary oryx bulls, probably turned out of the herds by more vigorous rivals, and often one of these would be found with a herd of zebras which proved more tolerant of it than its own kinsfolk. All of this game of the African plains is highly gregarious in habit, and the species associate freely with one another.

Domestic Animals.—With but a single exception—the domestic cat—every animal which man has succeeded in subjecting to his uses has been a gregarious form and hence dependent upon its fellows for aid and succor. This, as may well be imagined, is a very potent factor in man's favor when he attempts the subjugation of a wild animal, for he, in large measure, supplies the need of kinsfolk and when the creature becomes dependent upon him the victory is half won. The surly, intractable individuals among male elephants, horses, and cattle would possibly be outlaws from their own kind in a state of nature. The independent habits of the domestic cat which Kipling has so admirably satirized in his story of "the cat that walked by its wild lone," are due to the non-gregarious character of its wild progenitors, and are attributes which centuries of domestication have never wholly eradicated. Hence the cat is always a guest, the other domestic animals becoming members of the family. The cat is more concerned with its surroundings than with its human associates. In war-torn France the dogs always went with the human refugees, while the cats remained behind and were sometimes found living amid the ruins when the repatriated family returned.

Communalism

Communalism, as has been said, always implies division of labor, sometimes with physical differentiation, although in higher organisms increased intelligence may offset physical differences, the individuals being more adaptable to the various tasks of the community and not necessarily limited to one or two. True communalism is found in but two groups of organisms, the insects and mankind; in each instance the final culmination of a long and important evolutionary line.

Insects

Among insects two orders only are sufficiently advanced to include communal forms: the Isoptera, termites or "white ants," and the Hymenoptera, ants, bees and wasps.

Termites (Fig. 31) are insects of a comparatively low grade of organization and bear no relationship whatever to true ants, their popular designation, "white ants," having arisen from the fact that, like the former, they dwell in large communities with a complex social system. Members of the two groups of insects

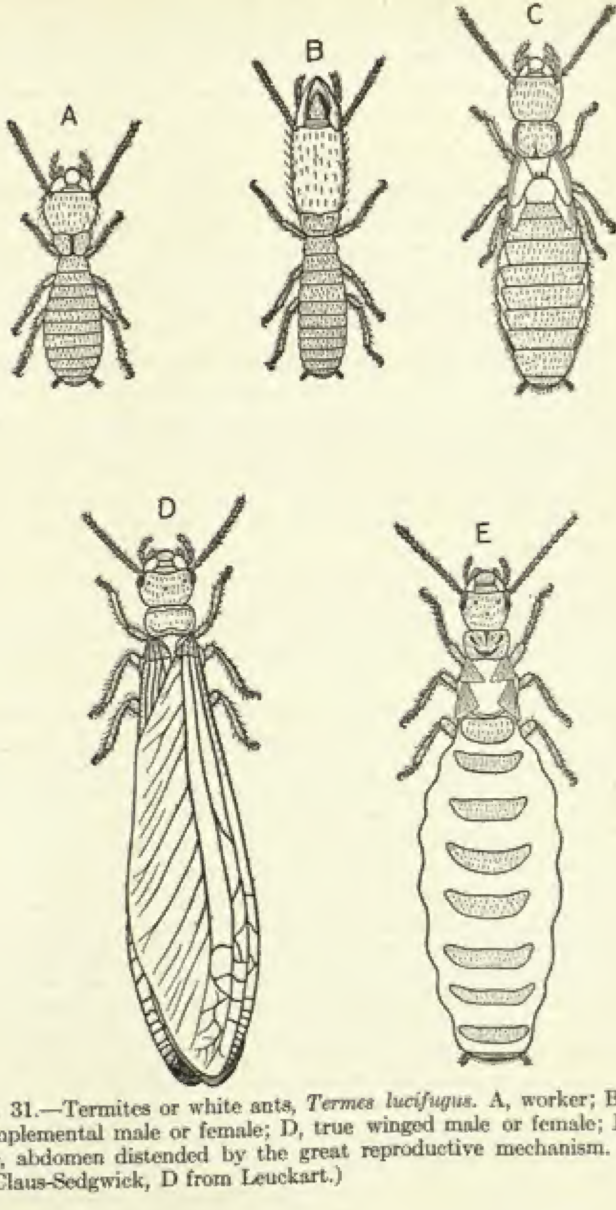

FIG. 31.—Termites or white ants, *Termes lucifugus*. A, worker; B, soldier; C, complemental male or female; D, true winged male or female; E, gravid female, abdomen distended by the great reproductive mechanism. (A-C, E, from Claus-Sedgwick, D from Leuckart.)

may readily be told apart, as the termites lack the delicate peduncle that joins the thorax and abdomen in the ants, and are broad-waisted creatures, yellowish white to light brown in color. Most of the termites are wingless, others have wings for a while which are afterward shed, many are blind, and all have slender antennæ resembling strings of beads.

Their social organization has carried with it a remarkable physical differentiation so that at least four distinct castes are generally recognizable; they are not, however, as in the case of the Hymenoptera, characterized by sex differences but include both males and females in each grade. The four castes are:

First, the *workers:* small, blind, wingless, pale in color, with undeveloped sexual organs, but with fairly well-formed jaws. In some species there are no workers, in others there may be two kinds.

The second are the *soldiers.* These are also blind and wingless and sexually undeveloped. Their chief distinction from all the other castes lies in the greatly developed scissors-shaped jaws which, together with the enlarged head, are darker in color than the rest of the body, due to their being more strongly armored.

The third caste consists of the *complemental males and females*, also blind and wingless, but with limited powers of procreation; otherwise they look not unlike the larger workers. Their duty is to supplement the production of young in the event of failure on the part of the chief sexed individuals.

The fourth caste are the *true or chief males and females.* These differ markedly from the other castes in their darker color and in being possessed of both wings and organs of vision, as they alone are concerned with the external world, all of the others being subterranean creatures which so far shun the light and air as to build covered tunnels for communication where burrowing is impracticable. The true sexed individuals are produced in great numbers, and in the spring emerge from their underground fastnesses and swarm forth on their mating flight. They are assailed by birds and other insectivorous creatures and countless numbers are destroyed before a suitable haven is reached. Ultimately they settle to the ground, such as survive the slaughter, and the wings are stripped off, breaking at a line of least resistance, so that only a stump remains behind.

The males and females now pair and each pair under normal conditions are the potential founders of a new colony. The supposition is that they must be found by a group of workers, who then take possession of them and make them the royal, or more properly parental, pair of a new community which these workers establish. Just how new colonies are formed in the familiar New England species, *Termes flavipes*, is not known, nor has a gravid true female ever been found, and it is within the possibilities that in spite of their numbers none of the chief caste ever succeed in surviving the mating flight, and that the young are produced entirely by the

complemental caste. Among tropical species—and they are very numerous, especially in Africa (see Drummond) and South America—the chief females, sometimes distended with eggs to many times their original size,[1] are frequently found.

The young are all alike when first hatched, three moults being necessary to develop into large-headed individuals, and three more to form the latter into perfect soldiers.

The termites have as commensal guests within their colonies many other kinds of insects of which more than a hundred species have been described. These are known as termitophiles or lovers of termites. The true ants have similar myrmecophiles, of which there are many more than in the present instance.

Hymenoptera show all gradations of development from solitary forms to those among which there is a most intimate communal life. Gradational series may be illustrated by the bees and wasps. The ants, on the other hand, are entirely communal.

Bees may be classified on the basis of habit and physiological development into three groups, solitary, gregarious, and communal, of which the hive bees have attained the highest development. The solitary bees need not be discussed, but as the social organization in the gregarious bees grades into the communal, a few may be described. Some of the technically solitary bees have a marked preference for one another's company and thus show the beginnings of gregarious life. Near Stanford University there is a huge colony of a mining bee, *Anthophora stanfordiana*, in which the vertical burrows are set as closely together as possible without interference, each burrow being the property of a single female bee. In this instance the hole is not filled with stored food and closed up as is usual, but the mother bee brings sustenance to the larva during its entire period of helplessness.

Andrena, the small mining bee, forms similar colonies; one recorded village which covered only a square rod of ground including several thousand nests. Here a vertical tunnel is dug with individual cells branching out on either side, within which the eggs are laid, together with a portion of suitably prepared food, the

[1] In a tropical African species, *Termes bellicosus*, the soldiers are fifteen times as large as the workers, and the fertile queen has her abdomen so enlarged and stretched by the thousands of eggs forming inside that it comes to be fifteen hundred or two thousand times the bulk of the rest of her body, and twenty or thirty thousand times the bulk of a laborer. The egg-laying capacity of such a female is given as sixty a minute, or eighty thousand and upward in one day of twenty-four hours (Kellogg).

cell being then sealed. The mother, having completed her domestic arrangements, waits in the mouth of the burrow for the issuance of the young.

With yet another mining bee, *Halictus*, the smallest of all, while each mother makes her own nest-burrow with its stored cells, a number combine to form a common vertical passage to the open air, so that one entrance and corridor give access to a number of homes. Many such structures are placed close together in populous communities. Thus, as Comstock says, "while *Andrena* builds villages composed of individual houses, *Halictus* makes cities composed of apartment-houses."

In bumblebees the domestic economy is similar to that of the wasps, the colonies, for such they are, lasting but a season. These bees pair in the fall, the males die, and the impregnated females pass the winter sleeping in some underground crevice or hole. In the spring they issue forth and gather pollen and honey which is mixed together into a pasty mass and placed in some underground hole, that of a mouse or mole or one which the bee digs for herself. Several eggs are laid upon the mass of food, the resultant larvæ feeding thereon until they are full-grown, when each spins a silken cocoon within which it passes through the pupa state to emerge as a sterile worker bee. These workers then take over the labor of the nest, enlarging it and providing more food, and the mother simply lays eggs to the extent of several sexually sterile broods. In late summer or fall males and females are produced which fly forth and pair. Then the males and workers gradually die off until only the pregnant females are left—the potential founders of next year's communities.

"The strange case of the guest bumblebees, species of the genus *Psithyrus*, is almost sure to come to the attention of any observer of bumblebee nests. In all general characters and total seeming truly bumblebee-like, found always in and about bumblebee nests, these insidious guests, cleverly living at the bountiful table of their host, present to us an interesting problem touching their deceptively *Bombus*-like makeup. Are they really bumblebees, that is, bees directly descended from bumblebee stock, which have become degenerate and adopted a parasitic life, or are they bees of another stock, which, for the sake of successfully deceiving the bumblebees and thus gaining access to their nests, have gradually acquired (through long selection) the bumblebee dress and general appearance? The former supposition is the more probable. They are like bumblebees in so many structural details unnecessary for such deception that they must be looked on as a degenerate offshoot from the Bombidæ. Having given

up the gathering and carrying of pollen, their tarsi are no longer provided with a pollen-basket (concave smooth surface, bounded by lines of long stiff incurving hairs) and by the absence of this arrangement they may always be distinguished from the true bumblebees. There is no working caste, infertile female workers, with these Psithyridæ, each species being represented by males and females only" (Kellogg).

The honey or hive bees, *Apis mellifica* (Fig. 32), differ from the bumblebees in that the colonies are permanent and composed of a much greater number of individuals. These live in their wild state in a hollow tree, although those found wild in America are all escaped domestic swarms. The numbers in a colony vary from ten thousand in winter to fifty thousand in summer, of which but one individual is a fertile female, possibly several hundred are male or drones, and the rest sexually immature females or the workers, all three sorts being anatomically distinguishable. The queen is merely the mother, never working or gathering honey as

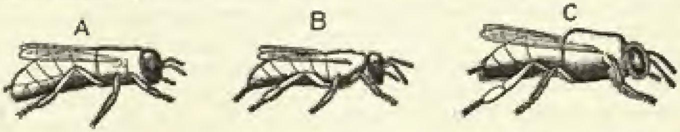

FIG. 32.—Honey bee, *Apis mellifica*. A, queen (perfect female); B, worker (imperfect female); C, drone (male). (After Brehm, from Parker and Haswell.)

with the bumblebees, while the drones act as consorts for the queen, only one in a thousand, perhaps, performing any real function for the colony at all. The workers "build brood- and food-cells, gather, prepare, and store food, feed and otherwise care for the young, repair, clean, ventilate, and warm the hive, guard the entrance and repel invaders, feed the queen, control the production of new queens, and distribute the species, founding new communities, by swarming" (Kellogg). Although the colony is permanent, its members die just as in human communities. The workers which hatch and labor in the spring and summer rarely live more than six or eight weeks, while those born in late autumn may survive the winter. Queens live from two to three, even five years, while the drones all die or are killed by the workers before the coming of winter. Feeble workers, larvæ, and pupæ are generally also slain.

The ants, of which the total number of species has been estimated to be at least 5000 (Wheeler), are without exception communal, and have carried their societal evolution further than any

other animal, not even excepting the lower races of mankind. Wheeler says of them:

"Ants are to be found everywhere, from the arctic regions to the tropics, from timberline on the loftiest mountains to the shifting sands of the dunes and sea-shores, and from the dampest forests to the driest deserts. Not only do they outnumber in individuals all other terrestrial animals, but their colonies even in very circumscribed localities often defy enumeration. Their colonies are, moreover, remarkably stable, sometimes outlasting a generation of men. Such stability is, of course, due to the longevity of the individual ants, since worker ants are known to live from four to seven and queens from thirteen to fifteen years. In all these respects the other social insects are decidedly inferior. . . . Not only do the ants far outnumber in species all other social insects, but they have either never acquired, or have completely abandoned, certain habits which must seriously handicap the termites, social wasps and bees in their struggle for existence. The ants neither restrict their diet, like the termites, to comparatively innutritious substances such as cellulose, nor like the bees to a very few substances like the honey and pollen of the evanescent flowers, nor do they build elaborate combs of expensive materials, such as wax. Even paper as a building material has been very generally outgrown and abandoned by the ants. Waxen and paper cells are not easily altered or repaired, and insects that are wedded to this kind of architecture, not only have to expend much time and energy in collecting and working up their building materials, but they are unable to move themselves or their brood to other localities when the nest is disturbed, when the moisture or temperature become unfavorable or the food supply fails. The custom of depending on a single fertilized queen as the only reproductive center or organ of the colony has also been outgrown by many ants. At least the more dominant and successful species have learned to cherish a number of these fertile individuals in the colony. Finally, the manifold and plastic relationships of ants to plants and other animals are in marked contrast with the circumscribed and highly specialized ethological relationships of the social bees and wasps. The termites undoubtedly resemble the ants most closely in plasticity, but . . . these insects, too, are highly specialized, or onesided in their development. This is best seen in their extreme sensitiveness to light, for this practically confines them to a subterranean existence and excludes them from many of the influences afforded by a more varied and illuminated environment."

The social evolution of the ants parallels in a very remarkable way that of mankind and from this point of view they may be classed as foraging, herding, and agricultural ants, with lesser groupings as well.

1. *Foraging or marauding ants.* The genus *Eciton*, the so-called driver ants, best illustrate this stage of savagery, especially on the part of certain Brazilian species in which, in their long marches in search of booty,

the great army is said to be marshaled by big-headed officers and led by scouts! These ants make their expeditions to the nest of other ants for the purpose of capturing the larvæ and pupæ which are used as food, and such as are not devoured are stored in the temporary nest, their captors being nomadic, and are used for some time after the foray is over. On their long marches they carry as booty the dead bodies of various insects as well as the helpless young of the pillaged ants.

2. *Slave-holding ants.* Slave-holding seems to be a natural outcome of the habit on the part of the marauding ants of bringing home the larvæ and pupæ of other ant colonies. Of course if all were devoured before emerging as adults, such a thing could not happen, but, as Kellogg says, the instinct of the hatched workers is to work, and so work they do; hence if any captives survived and their work was of advantage to the raider community, natural selection would do the rest. In the beginning there were no slave-makers but only raiders who raided for food, not for slaves. But by bringing home extra supplies of this food, which hatched and lived and worked in the new nest, evolution from food to slaves and from raiders to slave-makers has naturally taken place.

Some slave-making ants are now absolutely dependent upon their captives for all work done in the colony, and one, *Polyergus*, has gone so far that it can neither dig nor care for its young or even keep itself from starvation in an abundantly stored nest without the aid of its slaves. "Specialization is leading *Polyergus* to its end!"

3. *Herding ants.* These are in reality commensal forms living in beneficial association with other insects, notably the aphids or plant-lice. The ants, however, as one would suppose, are the masters and the aphids serve them as domestic cattle serve mankind. The economy can best be understood by a specific instance, that of the little brown ant, *Lasius brunneus*, which gathers the young larvæ of the corn-root louse in the fall and keeps them safe beyond the reach of any natural enemies until spring, when they are transported to the roots of certain weeds until the corn germinates, and then to the roots of the growing corn and herded there until mating time in the autumn, when they are allowed to pair and their offspring preserved as before. Other species gather various plant-lice eggs which they conserve during the winter, colonizing them upon their proper food-plants in the spring. In return for this care the ants secure from the aphids the so-called honey dew which exudes from two tube-like processes, the honey tubes or cornicles, projecting from the upper surface near the end of the abdomen. The plant-lice readily yield the honey dew to the ants, though in some cases the ants may not feed upon it directly but upon a fungus which in turn grows upon the sweetish exudation accumulating upon the surrounding leaves. Certain of the aphids seem to be utterly

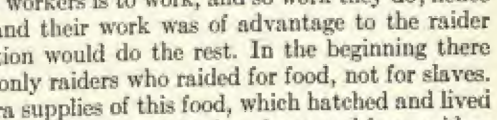

FIG. 33.—Red ant, *Formica rufa*. A, male; B, worker; C, female. (After Brehm, from Parker and Haswell.)

dependent upon the ants for their well-being if not for their very existence.

4. *Agricultural ants.* These harvester ants, as they are perhaps more accurately called, belong to the genus *Pogonomyrmex*, of which nine species occur in America, especially in the West and South. They form communities, usually of considerable size, the nests being partly below, partly above ground in the form of large symmetrical heaps in open sunny places, generally where there is more or less grass. The nests are stored with seeds and grains, garnered from the surrounding grasses which are cut away in the area immediately contiguous to the nest. From this bare area well-worn trails diverge into the surrounding grass. The harvester ants have been said actually to plant their favorite grasses, especially that known as ant rice or *Aristida*, to the exclusion of other crops. This Wheeler has shown to be untrue, but a voluntary planting is simulated by the fact that chaff or sprouted seeds, which would be valueless as winter rations, are removed from the nest and dropped at the edge of the cleared circle and in many instances take root and grow, resulting in an unintentional sowing of seed, and as *Aristida* seeds make up a large part of the food-stores, a majority of the plants about the nest may be *Aristida*.

5. *Honey ants.* There is a species, *Myrmecocystus melliger*, found in the semi-arid West, which McCook has especially studied in the Garden of the Gods, Colorado, where their mounds occur in hundreds. Certain of the workers through a curious structural modification may become greatly distended with honey so as to be as large as a small grape. "These honey-bearers hang by their feet from the ceiling of small dome-shaped chambers in the nest; their yellow bodies stretch along the ceiling, but the rotund abdomens hang down as almost perfect globules of transparent tissues through which the amber honey shines. The honey is obtained by the workers from fresh (growing) cynipid galls on oak-trees, which exude a sweetish sticky liquid which is brought in by foraging workers and fed to the sedentary honey holders by regurgitation. It is held in the crop of the honey-bearer, the distention of which produces the great dilation of the abdomen. The stored honey is fed on demand to the other workers by regurgitation; a large drop of honey issues from the mouth of the honey-bearer, resting on the palpi and lips, and is eagerly lapped up by the feeding individuals, two or three often feeding together. A somewhat similar honey ant, *Prenolepis imparis*, is common in California."

6. *Thief ants.* These are abundant tiny creatures, belonging to the species *Solenopsis molesta*, which live in association with several different species of larger ants, feeding upon the larvæ and pupæ, so that they are in a sense marauder ants, of which we have already spoken. The smaller galleries of the thief ants lie beside the larger ones of their hosts and occasionally open into them, so that the burglarous creatures, which are small and obscurely colored, can carry on their depredations with impunity, escaping into their own galleries, which the larger ants cannot enter, whenever they are detected and pursued.

7. *Commensal ants.* These also live at the expense of associated species, but apparently give some return for the benefits enjoyed, which the thief

ants do not. One such instance, recorded by Wheeler, is that of the common red-brown ant *Myrmica brevinoides* and the smaller *Leptothorax emersoni*. "The little Leptothorax ants live in the Myrmica nests, building one or more chambers with entrances from the Myrmica galleries, so narrow that the larger Myrmicas cannot get through them. When needing food the Leptothorax workers come into the Myrmica galleries and chambers, and, climbing on to the backs of the Myrmica workers, proceed to lick the face and the back of the head of each host. A Myrmica thus treated 'paused,' says Wheeler, 'as if spellbound by this shampooing and occasionally folded its antennæ as if in sensuous enjoyment. The Leptothorax, after licking the Myrmica's pate, moved its head around to the side and began to lick the cheeks, mandibles, and labium of the Myrmica. Such ardent osculation was not bestowed in vain, for a very minute drop of liquid—evidently some of the recently imbibed sugar-water—appeared on the Myrmica's lower lip and was promptly lapped up by the Leptothorax. The latter then dismounted, ran to another Myrmica, climbed onto its back, and repeated the very same performance. Again it took toll and passed on to still another Myrmica. On looking about in the nest, I observed that nearly all the Leptothorax workers were similarly employed.' Wheeler believes that the Leptothorax get food only in this way; they feed their queen and larvæ by regurgitation. The Myrmicas seem not to resent at all the presence of the Leptothorax guests, and indeed may derive some benefit from the constant cleansing licking of their bodies by the shampooers. But the Leptothorax workers are careful to keep their queen and young in a separate chamber, not accessible to their hosts. This is probably the part of wisdom, as the thoughtless habit of eating any conveniently accessible pupæ of another species is wide-spread among ants" (Kellogg).

Mankind

The evolution of mankind forms the subject-matter of later chapters. He is to-day, especially in his more highly civilized state, the final product of communal life, for while much may be accomplished by man as an individual, it is only in coöperation with his fellows that his great supremacy over the brute and physical creation may be manifest. None of man's relatives among the primates are more than gregarious, and it is probable that, until the descent of the human precursor from the arboreal habitat, he was but gregarious also; terrestrial existence only permitting the development of true communal life. If this be true, his communal coöperation can hardly antedate the Pliocene and may well have had a still more recent beginning. Our fossil records show that of the two groups of insects whose societal evolution compares with that of man, the termites were physically perfected

by early Eocene, the ants during Oligocene time. The presumption is therefore that their evolution since these several dates has been purely societal. If this be true, their communal life in each instance antedates that of the sentient head of the animal kingdom itself, a fact which entitles these humble creatures to increased respect.

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CHAPTER XVII

PARASITISM AND DEGENERACY

We have spoken in an earlier chapter (Chapter II) of the mutual dependence of associated organisms upon each other for protection, transportation, and food. Where this is a mutually beneficial partnership, we have called it commensalism or symbiosis, but where one of the partners is unwilling and the benefit of the association is all with the other, it is called parasitism. Undoubtedly certain of these partnerships lie on the border line, and it seems equally true that many cases of true parasitism have arisen out of a benign association.

Creatures which are not free-living, but depend upon others directly for their food are extremely numerous, and of these the ones bearing the relationship of parasite to host number, according to one authority (Eccles), more than half of all the animal creation. Hence as a means of adaptation for survival, parasitism must be looked upon as a remarkably successful device, although the resultant evolution may often be one of retrogression and ends in greater or less degeneracy according to the degree of parasitism and the relative rank of the animal at the beginning of its degenerating career.

Bionomic Classification of Parasites

Aside from their natural taxonomic rank in the animal or plant kingdom, parasites may be divided bionomically into the following groups.

First, as to duration, parasites may be either Temporary or Permanent.

Temporary or partial parasites are the creatures which, like many insects, are parasitic during but a portion of their life and free-living at other times. In some cases it is the adolescent which has become parasitic. This is true of the parasitic Hymenoptera, whose eggs are laid by being thrust by means of a special device (ovipositor) into the body of another insect, a caterpillar for instance, within which the entire larval state is passed, the parasite feeding

as a rule on the fat-body or other non-vital portions of its host. When its larval time is fulfilled, the parasite emerges through the body-wall, spins a tiny cocoon on the outside of its host, within which it pupates, and finally emerges as an adult fly of free life and habits totally distinct from those of its young. Another instance of a temporary parasite is the ordinary dog or cat flea, this time parasitic as an adult, living its adolescent life in the cracks of the floor where sufficient organic material is usually found to give it sustenance. Those whose parasitic career embraces the adult condition, as in this instance, show greater degeneracy than those parasitic as young, for the higher the animal is, the greater the fall, and an adult has generally attained a loftier plane of development than its young.

Permanent or total parasites are such as have practically no free stage in their career, like the dreaded trichina worm to be described later on. This creature is found encysted in the flesh of one host and passes to the next through the latter having eaten of the first, and normally an indefinite number of generations may live their lives without ever being in the outer air. Permanent parasites are more frequently found among lower forms and always require a succession of similar hosts or a blood-sucking alternative host, while the great proportion of higher parasites are temporary.

Parasites are also classified as to degree into Facultative and Obligate.

Facultative or optional parasites are terms applied to the more adaptable sorts which, lacking their normal host, may turn to another, or even exist as free-living forms. Many parasites are facultative, although in some cases the new host may be closely related to the old.

Obligate or compulsory parasites, on the other hand, are the less adaptable sorts, and require a definite host or succession of hosts. It is questionable whether very many parasites are strictly obligate in the sense of requiring a restricted species. Certain tapeworms are such, however, the human tapeworm, *Tænia solium*, being derived from the flesh of the swine, while *T. saginata* has for its alternate host the domestic cattle, and their adaptation to the human intestine is so perfect that they cannot be made to live anywhere else, for repeated experiments with monkeys, dogs, cats, sheep, goats, pigs, and rabbits have failed to establish these worms within them (Petrunkevitch). The tuberculosis organism, on the

other hand, is facultative, with, unfortunately, a rather wide range of hosts.

The third grouping is with reference to the position of the parasite, whether upon or within the host.

External or superficial parasites, which confine their depredations to the outside of their host, are external or ectoparasites, such as the flea of which we spoke. External parasites, which are largely arthropods, may become degenerate but are rarely of such vital moment to the host *in themselves;* it is only when they in turn are parasitized and are thus the carriers of disease that they become a real menace.

Internal or intimate parasites (endoparasites) are many, and while a large number of them have retained the primitive simplicity of their free-living ancestors, many of those which are zoölogically high in the scale of life show a very marked degeneracy which is in some cases extreme. Many Protozoa, bacteria of disease, and especially worms of various sorts are included under this head. These intestinal parasites possess what is called an anti-body, which prevents their digestion by the fluids of the host, otherwise they would be thus destroyed.

Effect of Parasitism

On the Host.—The effect of parasitism upon the host is generally a harmful one with no compensating benefit. It does not invariably result fatally at once to the individual, but in many adolescent insects prevents their reaching the adult stage and therefore renders impossible the procreation of further generations. Again, it may either destroy or prevent the development of the sexual glands and in this way gives rise to the same result. In preserving the balance of nature, parasitism is undoubtedly one of the strongest factors, keeping naturally prolific creatures effectively in check. There is reason to believe that it has had much to do with the extinction of prehistoric races of animals, and Doctor Eccles has brought together some interesting data which bear upon this problem. He believes, and his observations are based upon extensive study of germ diseases, that apparently all animals of the present and past are infested by one or more parasites feeding upon the host, and that the parasites are themselves infected by parasites. This is known as hyperparasitism and has been actually observed to the fourth degree.

In the course of time the surviving hosts become immune to the parasites and all goes well until new migrants arrive, bringing new parasites and therefore new diseases into the area. The new disease will cause immense destruction until the native animals, or the survivors of them, again attain immunity. Therefore times of renewed migration, which, as we have seen in our discussion of animal distribution, are concurrent with the formation of new migratory routes—land-bridges, forest tracts, removal of old-time barriers, and so forth—should be times of disestablishment and economic disorganization.

Immunity to disease does not necessarily mean immunity to the parasite, but rather that the host has become capable of enduring the parasite within its system and at the same time showing every manifestation of perfect health. Nevertheless such an individual may be a carrier of the disease of the most insidious sort, as medical practitioners have learned to their sorrow. One notable instance in point is that of the cattle-infesting Texas fever which has been thus graphically described by Doctor D. E. Salmon. He says:

"The cattle which spread the disease are, themselves, apparently in good health, while the cattle that become sick do not themselves disseminate the contagion. Again, susceptible cattle might be mingled with impunity with cattle from the infected district, providing this mingling occurred immediately after their arrival, and did not continue longer than two or three weeks; while, on the other hand, susceptible cattle that later in the season trespassed for even a few minutes on the pastures where the infectious cattle had been would contract a most violent form of the malady. . . . Texas fever is caused by a microscopic parasite, which lives within the red globules of the blood. The cattle in the infected district carry this parasite permanently, and are so nearly immune to its effects that they remain in good health, notwithstanding its presence in their blood. Not so, however, with cattle which never before have encountered it. With such animals it destroys the red corpuscles and reduces them to one third or one fourth the normal number. An intense fever is produced, and the creatures rapidly waste away and die after a sickness of one or two weeks."

The East Coast fever of Africa, which is very similar, is caused by a very closely related parasite which likewise lives in the red corpuscles of its host. Infected East Coast cattle show no ill effects, but are "carriers" of the disease. Non-immune cattle brought into the East Coast region are open to certain attack, and the assertion has been made that out of each hundred which are thus assailed but five on the average survive. In one epidemic, due to the

introduction of infected animals into the Transvaal, 15,000 cattle died. In trypanosomiasis (sleeping sickness) we have another instance of this same condition. Notwithstanding the fact that there may be no sick animals in the fly country of Africa, no horses, cattle or dogs can venture, even for a day, into the region. Most of the wild animals, however, the buffalo, koodoo, and wildebeeste or gnu, carry the trypanosomes in small numbers in their blood, and it is from them that the tsetse fly obtained the parasite. The wild animals act as reservoirs of the disease. The trypanosome seems to live in the blood of the wild animals without doing them any manifest harm, but when introduced into the blood of such domestic animals as the horse, the dog, or the ox, the victims rapidly sicken and die.

Fig. 34.—Parasite which causes disease among cattle, *Trypanosoma theileri*, from the blood of cattle in Transcaucasia, × 3000. (After Lühe, from Calkins.)

On the Parasite.—The effect of parasitism on the parasite, which may be much or little, on the part of the higher forms at least is invariably one of degenerative specialization, the parasite being below the standard of its free-living congeners. Of course, simple ancestors imply little or no degeneracy; on the other hand, the retrogression may be profound if the parasite be one of high descent. In temporary parasites the alteration may not be so decided as in permanent ones, but it varies with the degree of adaptation to parasitic life.

Parasitic organisms, like sedentary forms, are apt to lose their organs of locomotion and develop instead structures for attachment or adhesion, such as tentacles, hooks or suckers. Correlated always with the diminution of locomotive powers is that of the

organs of special sense, the only sense remaining in extreme instances being the tactile, which is a primordial function of protoplasm itself. The nervous system as a whole shows degeneracy. There may also be a simplification of the external skeleton as in arthropods, especially if the parasite be internal.

Parasitism often means reduced metabolism and a consequent reduction of the vegetative organs, such as those of respiration and circulation, and especially of the alimentary canal, wherein the digestive glands are the first to disappear, for, as in certain intestinal worms, notably *Ascaris*, the organism lives virtually in predigested food which only awaits absorption. In the tapeworms the extreme is reached, for in them there is no trace of alimentary canal at all, the nutrient medium in which the animals live being absorbed directly through the body-wall of the flattened degenerate.

The reproductive organs alone suffer no diminution, but on the contrary may become still more highly developed, especially among internal parasites, for among these in particular the vicissitudes attending the organism during its life cycle and especially during its migration from host to host are great, and fecundity must needs be proportionately increased. Hermaphroditism frequently characterizes the parasite and in some instances self-impregnation seems to occur. Parasitic plants lose many organs but never the blossoms, which are often of wondrous beauty, as for instance, certain of the orchids.

Value of Recapitulation

Were it not for the assumption, therefore, that the life history of the individual tends broadly to summarize the evolution of its race, and that the earlier stages in ontogeny may repeat those in the phylogeny, taxonomic (*i. e.*, zoölogical or botanical as opposed to bionomic) classification of some parasites would be virtually impossible. For example, in the crab parasite, *Sacculina* (Fig. 35), we see so extreme a state of degeneracy that the creature is reduced to a condition not unlike that of a tumor growing on the under side of the host's abdomen (see Fig. 35,C). Dissection shows this tumor to possess nothing comparable to an alimentary canal, but in its stead a large growth of ramifying processes, like rootlets, extending through every portion of the crab's anatomy, even to its eyes, and serving to extract nutritive juices just as the rootlets

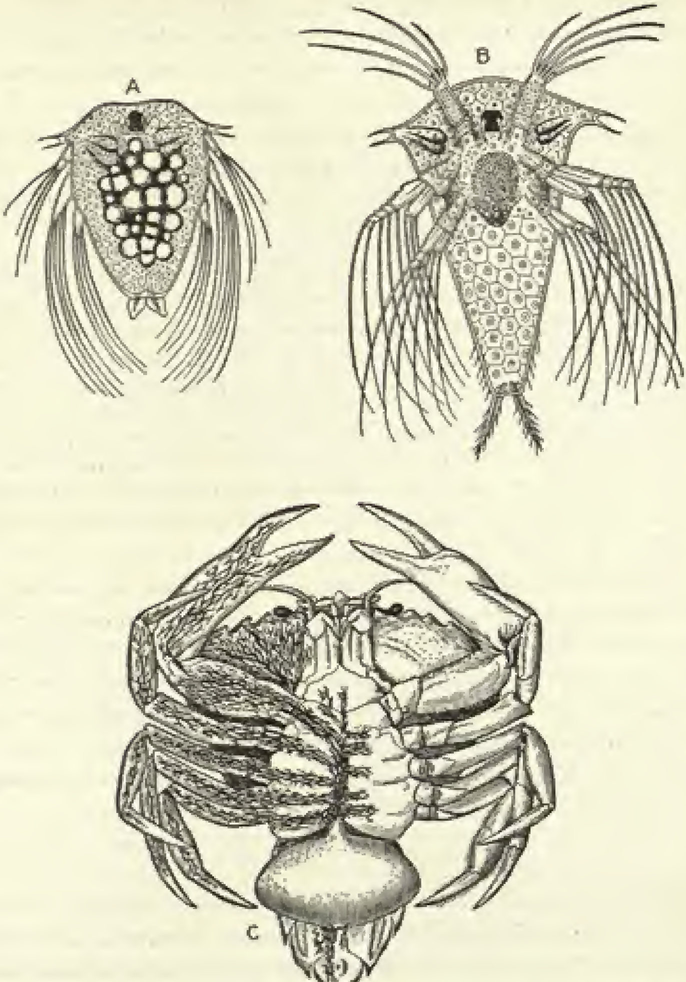

FIG. 35.—The nadir of parasitism, *Sacculina carcini*. A and B, larval (nauplius) stages; C, crab, *Carcinus mænas*, with a mature *Sacculina* in situ, showing ramifying "roots" (omitted from left side) which extract nourishment from the crab. (After Delage, from Leuckart.)

of a plant absorb nourishment from the soil. Within the body of the parasite are a decidedly reduced nervous system and enormously developed reproductive organs. Such is *Sacculina*, and as such its classification is impossible until its life history is revealed, when its taxonomic rank is at once manifest.

Sacculina is at the nadir of parasitic degeneration. But what of the life history? Out of the brood chamber there emerge Nauplius-larvæ, with three pairs of appendages, without food-canal but possessing a median eye. They pass into the second—a blind Cyprid larval stage. These fix themselves, just like barnacles and acorn-shells, by means of their first pair of feelers, to the back or limbs of young crabs, finding a soft place at the base of the large bristles or setæ. All but the head region is cast off; the structures within the head contract; eyes, tendons, pigments, and the remains of the shell are all lost; and a tiny sac sinks into the interior of the crab. Eventually it reaches the ventral surface of the abdomen, and, as it approaches maturity, the cuticle of the crab softens beneath it, so that the sac-like body protrudes. It seems to live for three years, during which the growth of the crab is arrested. The reproductive organs of female crabs are partially or completely destroyed, while the males either take upon themselves female characteristics in varying degree or become actually hermaphroditic (Thomson).

The life history of *Sacculina* up to the time of its fixation is therefore essentially as in other barnacles, hence its inclusion with them in the order Cirripedia. And the larval stages—the Nauplius and Cypris—are found in many other Crustacea, and therefore the barnacles are included within that class. As adults the diagnostic crustacean features are certainly conspicuously absent in *Sacculina*, so that it may be said of them, although in a perverted sense, "By their fruits ye shall know them."

Examples of Parasites

Sporozoa.—One group of Protozoa, the class Sporozoa, is composed exclusively of parasites. It is possible, therefore, that their general similarity, shown in the absence of locomotor organs and in their mode of reproduction by means of spores, may be due to convergent characters resulting from their parasitic mode of life. In other words, instead of a natural group of related organisms, we may be dealing with a heterogeneous assemblage derived from several more or less remote ancestral stocks. The Sporozoa are all internal parasites, some of which inhabit the digestive tract of their host, others the cœlome or body cavity, others the cells, and yet others find lodgment in the very nuclei of the cells themselves.

Finally, some are blood-inhabitants. In many cases there may be modifications of these several modes of life or combinations of them. Of such is the malaria organism, the genus *Plasmodium*, several species of which give rise to the disease known as malaria in the human being. The three undoubted species are *Plasmodium vivax*, producing tertian fever in which there is an attack every forty-eight hours; *Plusmodium falciparum*, giving rise to the pernicious autumnal or malignant malaria characterized by daily or more or less constant fever; and *P. malariæ*, producing quatrain fever which gives rise to paroxysms every seventy-two hours. The significance of these attacks is that they coincide with the periods of schizogonous (Gr. σχίζειν, to split) reproduction of the parasite, during which it migrates to new blood corpuscles. At such times there is a decided anemia and poisoning which give rise to fever and other bad conditions due to the impoverishment of the blood. Even death may ensue. The parasite therefore reproduces by the formation of "spores," but ultimately, sex elements, male and female, may be developed; actual sexual reproduction does not, however, occur in the human host. If the person is then bitten by an Anopheles mosquito, the latter's digestive fluids destroy all of the malaria organisms contained in the extracted blood except such as are in this sexual stage. These then pair and the fertile cell bores into the walls of the mosquito's gut where it gives rise to many spores which are finally liberated into the body cavity, whence they are carried by the blood to the salivary glands and there come to rest. Upon biting another person, the mosquito injects a tiny portion of saliva into the wound—hence the sting—and with the saliva comes the malaria germ.

As these organisms are all of the same brood, their subsequent periods of reproduction coincide, so that a constantly increasing number of spores is liberated at stated intervals, depending upon the species, until ultimately the numbers are incredibly large, and the effects upon the patient proportionately severe. *Plasmodium* is therefore a permanent, obligate parasite, but as its ancestors were lowly forms, there is probably no very marked degeneracy as a result of its parasitic adaptation.

Worms.—Among the roundworms, Nemathelminthes, there is a very terrible human parasite with a relatively simple life history. This is *Trichina spiralis*, a somewhat facultative type, as it has been recorded from the rat, dog, cat, pig, and man. *Trichina*

(see Fig. 36) lives encysted in a state of quiescence in the voluntary or skeletal muscles of its host. Each worm is coiled in a characteristic spiral within the limits of a single muscle fiber, and is surrounded by a small, limy, lemon-shaped cyst. If the host is eaten by another—the imperfectly cooked pig, for instance, by man—the acid of the gastric juice dissolves the cysts and liberates the worms. These are of separate sexes and immature, but they soon grow up, pair, and the females give birth to a thousand offspring each. These bore through the walls of the stomach and are

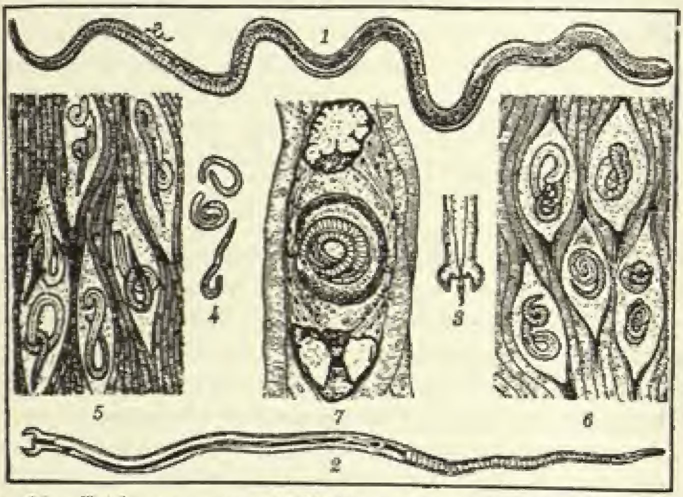

FIG. 36.—*Trichina spiralis* embedded in muscle. 1–3, *Trichina* in the intestine of the pig; 4, Larvæ in the blood of the pig; 5–7, *Trichina* in muscle. 1, female, with living larvæ; 2, male; 3, same, showing hinder end with copulatory organ; 5, *Trichina* in muscle, not yet encysted; 6, same, encysted; 7, beginning of calcification of the cyst. All greatly enlarged. (After Esokor and Fiebiger, from Doflein.)

carried by the blood stream to adjacent voluntary muscles such as the diaphragm. Here the creatures enter and pass between the muscle-fibers for a certain distance and finally pierce the membrane surrounding some one fiber, enter, coil, secrete the surrounding cyst, and the life cycle is complete. An ounce of infected pork has been estimated to contain 80,000 worms of which perhaps half are females, and if each produces 1000 young, the surprising total of 40,000,000 worms may be derived from a single ounce. The trichina population of a diseased man has been calculated to equal 100,000,000—the population of the United States in 1915! After

encystment is accomplished, the patient, if he has survived, recovers, but grievous symptoms diagnostic of the disease trichinosis are manifest during the period of parasitic activity and in a certain percentage of cases death ensues.

Trichina is a permanent parasite, never having a free-living stage; it does not, however, show marked degeneracy except that it is capable of withstanding long periods of quiescence—ten years at least, how much longer is unknown. Alternate hosts of different species are unnecessary, provided cannibalism exists.

Among the flatworms, Platyhelminthes, there are numerous parasites, of which one of the most interesting from the standpoint of its life history is the liver-fluke, *Fasciola hepatica*, which inhabits the liver and bile ducts of the sheep, deer, and certain other grazing animals. This is a rather large worm, as such forms go, at least an inch in length, flattened, leaf-like, and provided with suckers for attachment and the getting of food. The worms are hermaphrodite and the reproductive organs, both male and female, occupy a large portion of the animal's interior economy. They are thus highly prolific and their parasitical degeneracy is manifest in that they are self-fertilizing. The eggs thus produced pass down the bile ducts and through the intestine to the outer world, where each hatches into a minute larva, ciliated outside, and provided with eyes. The eggs soon die if the ground is dry, but if they fall upon moist ground they may survive for several weeks, and if into a pond the larvæ soon emerge in search of a new host.

This new host is a pond snail (*Lymnæus truncatulus* or *minutus*) or even a *Helix* will do, any of which *Fasciola* enters by way of the respiratory aperture. Established within the respiratory organ of the snail, the larva loses eye-spots and cilia and changes into a sporocyst, within which develop a number of bodies known as rediæ, which are asexually produced larvæ of a second sort, provided this time with digestive organs. Each redia usually gives rise to more rediæ, and these in turn to the third larval form known as cercariæ, which also have a digestive system, suckers, the rudiments of other organs as well, and a well-developed locomotor tail, so that the creature resembles superficially a minute tadpole. The cercariæ are no longer content with the snail for a host, but pass out of it, being distributed by its wanderings, leave the water, climb up a blade of grass, lose the tail, form over themselves a

flattened, circular, limy cyst and lie in wait for the sheep. The latter eat the grass, cyst and all, the cyst dissolves and the cercaria is liberated. It now passes up the bile duct from the intestine to the liver and grows up directly into a fluke. This very roundabout process is the only way whereby the parasite may be perpetuated within the sheep.

Several interesting biological principles are here illustrated: Generations of asexually produced forms for rapid multiplication, the precocious production of offspring by immature young (pædogenesis, from Gr. παῖς, child), the development of sensory and locomotive organs where the creature is free-living, and their absence and the substitution of adhesive suckers during parasitic existence, and, finally, as a mark of degeneracy, hermaphroditism and self-impregnation, the latter being avoided by nature in that it apparently defeats the original purpose of sex.

The tapeworms of the genus *Tænia* are curious, ribbon-like forms consisting of a head-like organ or scolex, provided with suckers and sometimes with hooks for attachment; beyond the scolex are a number of transverse constrictions which divide the animal into a great many sections or proglottids, each of which is a sexually complete hermaphroditic unit. There is no digestive system, for, as has been said, the creature feeds by absorbing the already digested food in the alimentary canal of its host; other organs, nervous and excretory, are present, but in common with other internal parasites the organs of procreation dominate those of every other system. No locomotor or sense organs are present, but the creature can make feeble worm-like movements. At about the two hundredth segment beyond the scolex, where they are produced by a process of transverse constriction (strobilization), the male organs begin to appear, and further back toward the hinder end of the body the female organs become mature in segments which were originally male. Pairing is effected, perhaps with the anterior proglottids of the same worm, and the other organs then become reduced, owing to the great development of the brood-chamber or uterus. The first completed eggs are found in the four hundredth to five hundredth proglottis and from this point backward they rapidly increase until a great number are contained in the much branched uterus. The ripe proglottids are detached and pass out of the host to the ground, where for a time they move by contraction. Within the eggs in the meantime the embryos have become rounded bodies each armed with six hooks (hexacanth embryos). If the proglottis or the eggs should now be taken into the alimentary canal of a pig, the second host, the hooked embryos become free and bore their way by means of the hooks until they reach the voluntary muscles, where they come to rest. Here they increase greatly in size and develop into the proscolex, containing a large cavity filled with a watery fluid. On the wall of the proscolex a hollow ingrowth

is formed, on the inner surface of which suckers and hooks characteristic of the head or scolex of the adult develop. Then the hollow ingrowth turns right side out, so that these organs come to lie on the outer surface. Thus the bladder-worm or cysticercus is formed, having a bladder-like expansion to which is attached a structure comparable to the head and neck of a mature worm. If the flesh of the pig is now eaten by man, without being

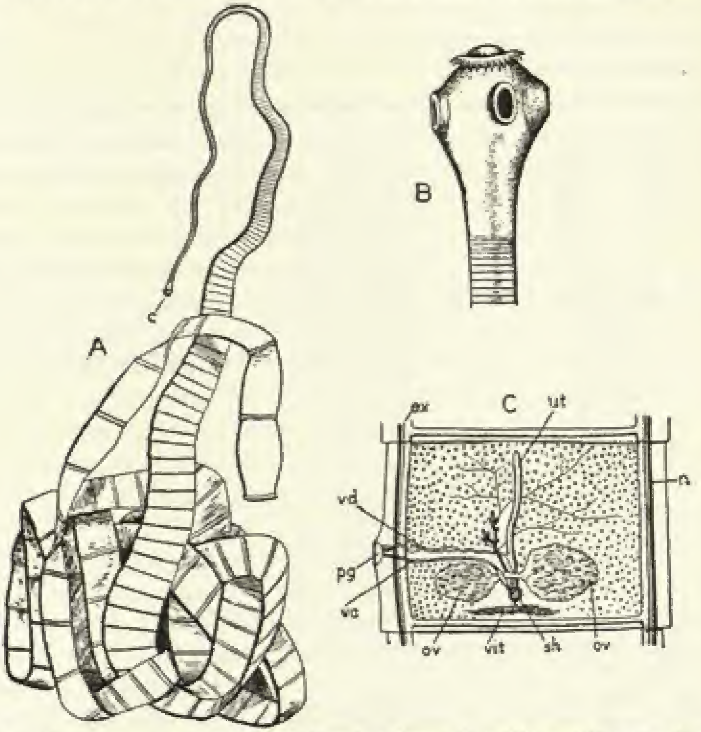

Fig. 37.—Tapeworm of the pig, *Tænia solium*. A, entire specimen, reduced: *c*, head; B, head or scolex, showing adhesive hooks and suckers, enlarged; C, proglottid or segment, enlarged, with mature reproductive apparatus: *ex*, excretory canal; *n*, longitudinal nerves; *ov*, ovary; *pg*, genital pore; *sh*, shell gland; *ut*, uterus; *va*, vagina; *vd*, vas deferens; *vit*, vitteline gland. (After Leuckart, from Parker and Haswell.)

adequately cooked or salted, the worm is liberated, the bladder abandoned, the head attached to the intestinal wall, and a new tapeworm developed. Except for the short period which the mature proglottids spend before being devoured by the swine, this parasite is entirely internal and in consequence shows marked adaptations for that sort of life and none whatever for life in the open. Its powers of multiplication are enormous. Petrunkevitch tells us that *Tænia solium* may live for from five to 15 years, during which time from two to five proglottids are broken off daily and pass out of

the host's alimentary canal. Each of these contains between 20,000 and 50,000 eggs, so that the yearly production may be as great as 18,200,000 and the total upwards of a quarter of a billion! In *Tænia saginata*, which is much more common, there may be as many as 1,368,750,000 eggs produced by a single worm, yet but one survivor is necessary for the continuation of the species, which shows how great a premium must be paid to insure perpetuation.

Crustacea.—The arthropods also embrace a host of forms which are parasitic—crustaceans, arachnids, and insects—and in the last there are parasitic forms in as many as five orders out of thirteen. Among Crustacea some curious instances may be cited, as in *Ergasilus* (Fig. 38,A), which is parasitic upon the gills of the bass. It is recognizable as a copepod crustacean, but parasitic adaptation shows in the modification of the antennæ into hooks for adhesion, reduction of legs, loss of eyes, and very large egg sacs. Another example is *Lernæa* (Fig. 38,D), in which, as in *Sacculina*, all trace of segmentation is gone and the feet are reduced to the merest vestiges. Its maxillæ are adapted for piercing the skin of the host and sucking its blood. The egg sacs are very large. *Lesteira* (Fig. 38,C), another copepod, is more degraded than *Lernæa*, adhering between the skin and flesh of a fish (*Genypterus blacodes*) by means of its swollen head, the rest of the body being

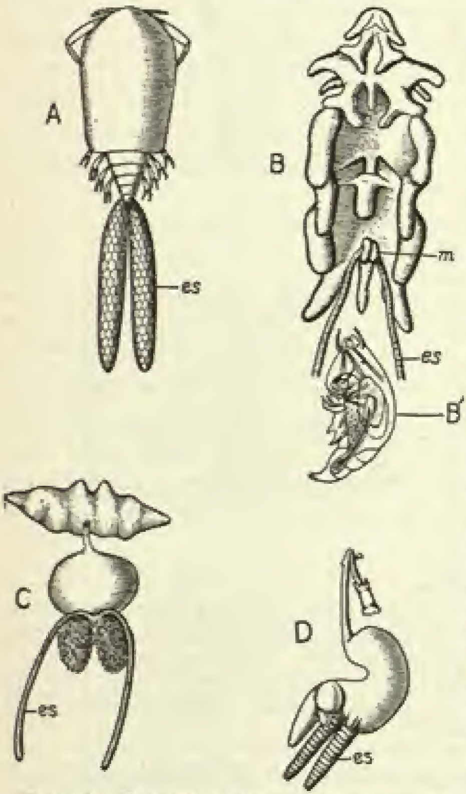

FIG. 38.—Parasitic Crustacea (Eucopepoda). A, *Ergasilus;* B, *Chondracanthus;* B′, same, male (*m*), enlarged; C, *Lesteira;* D, *Lernæa;* *es*, egg sacs. (After Parker and Haswell.)

free. *Chrondracanthus* (Fig. 38,B) has nothing to suggest a copepod except the characteristic egg capsules. The female is parasitic upon the gills of certain fishes and is curiously lobed. These lobes may, however, be recognized as antennules, hooked antennæ which serve as organs of attachment, mandibles, and two pairs of legs. The male is less degenerate but is permanently attached to the female, so that she is parasitic upon the fish and he upon her.

A much less degenerate parasite is that infesting the carp—*Argulus*, the carp-louse. While having special sucker-like organs for adhesion, which are modified limbs, it nevertheless crawls freely over its host.

Sacculina, the most degenerate parasitic crustacean, has already been described.

Insects.—Of insects which subsist wholly or in part upon other organisms there are hundreds of species, some remarkably degraded, others showing but little alteration from the organization of their non-parasitic allies. As one would expect, these latter are free-living as adults and only parasitic in their adolescent condition. Usually parasitism on the part of adults implies the loss of wings as in the bird-lice (Mallophaga), true lice, scale insects, fleas, sheep ticks, and the like. In one rather rare group (Strepsiptera), the creatures live upon bees and wasps as hosts during the larva and pupa state and in the female during the adult condition as well. The male, however, develops wings as an adult, otherwise, as these are solitary parasites, but one to a host, mating could hardly be effected.

In none of the parasitic insects are such complex life histories known as among the worms, although some of them, notably the lice and ticks, have evidently had a long parasitic career, as their adaptation is extreme.

Mollusca.—Among other invertebrates, the echinoderms and sponges have no undoubted cases of parasitism, although the sponge *Cliona* bores into the shells of living molluscs, which it subsequently destroys; and among the molluscs, parasitism is rare, as the creatures have met the demands of the struggle for existence in other ways which have proved fully as effective. One interesting instance of parasitism is that of the larva of the fresh-water clams *Anodonta* and *Unio*. Normally, pelecypod molluscs have a ciliated mero-planktonic larva, but in the fresh-

water forms they become parasitic in the way to be described. Fertilization is effected in the outer chambers of the female clam's gill and the developing young remain in this brood-pouch until it is distended with the tiny creatures held together by the entangling of the threads which are secreted by each larva. This mass is shortly expelled from the mother and lies on the bottom of the stream until it comes in contact with some passing fish, to which the young clams attach themselves by means of the hooked shell valves. *Unio* larvæ usually attach to the gills, *Anodonta* to the skin or fins. Here they become encysted by an overgrowth of the skin of the host and are nourished by its juices. They are thus true ectoparasites for a period of about ten weeks, at the end of which they have metamorphosed sufficiently to assume the normal free life of the clam. This parasitism evidently has for its major purpose the retention of the species in the rivers, for were the larvæ ordinary plankton like those of their salt-water relatives, the species could not maintain themselves in their flowing habitat, but would be swept out to sea beyond the possibility of return. Relative scarcity of microörganisms for food may be a secondary cause, but for the maintenance of habitat this parasitism is not only adequate but also justifiable.

Vertebrates.—The vertebrates include few true parasites among their numbers, though the degraded hag-fishes are on the border line between predatory and parasitic forms. There are, however, many instances of commensalism in some of which the mutual advantage may be quite unequal. Instances of vertebrate parasitism are the bitterling, a small, fresh-water fish, whose young are temporary parasites in the gills of mussels, and certain deep-sea angler fishes, in which only the females were known. Recently, however, the males were discovered, which after a brief period of normal freedom became degenerate parasites upon the body of the female.

Summary

Weismann thus summarized the problem of parasitism: "The most convincing proof of the organism's power of adaptation is to be found in the fact that the possibility of living parasitically within other animals is taken advantage of in the fullest manner, and by the most diverse groups, and that their bodies exhibit the most marvellous and far-reaching adaptations to the special conditions

prevailing within the bodies of other animals. We have already referred to the high degree reached by these adaptive changes, how the parasite may depart entirely from the type of its family or order, so that its relationship is difficult to recognize. . . .

"If we consider the number of obstacles that have to be overcome in existence within other animals, and how difficult and how much a matter of chance it must be even to reach such a place as, for instance, the intestine, the liver, the lungs, or even the brain or the blood of another animal, and when, on the other hand, we know how exactly things are now regulated for every parasitic species so that its existence is secured notwithstanding its dependence upon chance, we must undoubtedly form a high estimate of the plasticity of the forms of life and their adaptability. And this impression will only be strengthened when we remember that the majority of internal parasites do not pass directly from one host to another, but do so only through their descendants, and that these descendants, too, must undergo the most far-reaching and often unexpected adaptations in relation to their distribution, their penetration into a new host, and their migrations and change of form within it, if the existence of the species is to be secured."

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CHAPTER XVIII

ADAPTIVE RADIATION

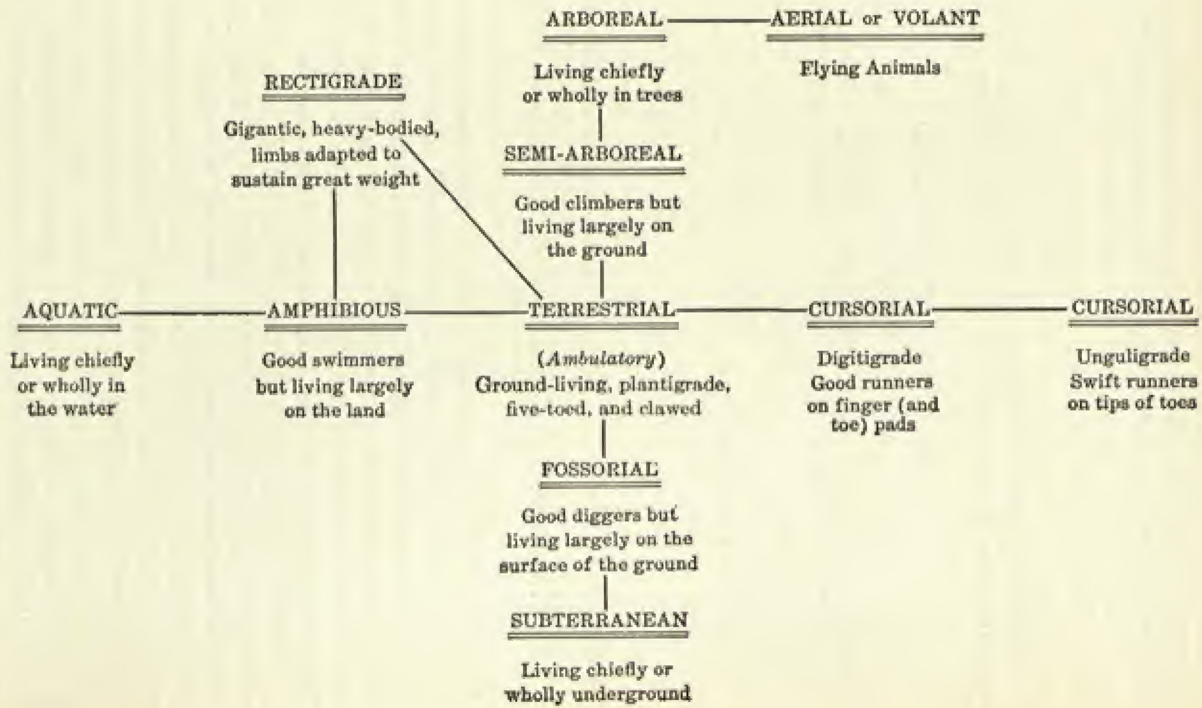
Adaptation to environment is one of the most obvious and at the same time remarkable qualities of living organisms; in fact, it sums up nearly the whole result of evolution, and the real cause of it all lies in the germ-plasm itself, although it is manifest only in the somatoplasm of the animal. Operating in dissimilar or unrelated groups whose life conditions are comparable, it has given rise either to parallelism or to convergence, so that animals of remote stocks have come to look and act alike in so remarkable a way that one sometimes imagines relationships where none actually exists. Such creatures have been called homoplastic (Gr. ὁμός, same + πλάσμα, anything molded, *e. g.*, by environment) in contradistinction to homogenetic (Gr. γένος, race) forms. Convergence is especially manifest in features concerned with locomotion, food-getting, offense, and defense.

The converse of this is known as divergence, where creatures of the same or closely related stocks have gone their several ways in their search for food and safety, giving rise to such varied adaptation that the several extremes of evolutionary lines depart markedly, not only from the norm or stem form, but also from each other. This idea of divergence under new and strange conditions is not new but was recognized by Lamarck, who called it "embranchement" and by Darwin, who used the term "divergence" itself to express the idea. Finally Osborn clearly stated it in the form of a law which he first called adaptive radiation. This law may be re-stated in his own words:

Law of Adaptive Radiation.—"Each isolated region, if large and sufficiently varied in its topography, soil, climate, and vegetation, will give rise to a diversified . . . fauna. The larger the region and the more diverse the conditions, the greater the variety of mammals which will result. From a primitive stem form radii go out in four diverse directions, the adaptations being mainly those of limbs and feet—also of teeth, but that of the teeth and feet do not necessarily parallel."

ADAPTIVE RADIATION

(ADAPTED FROM MATTHEW)

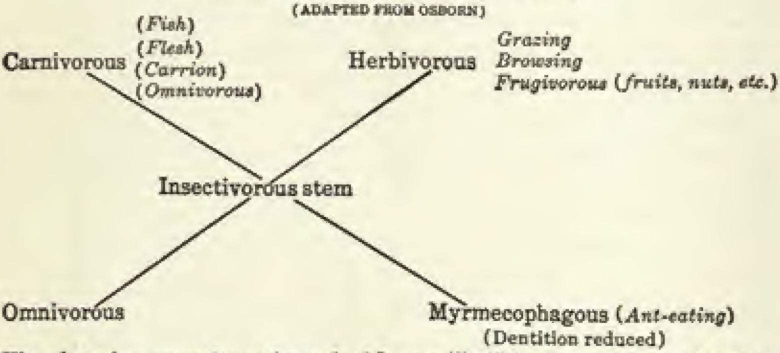


While the term adaptive radiation fairly describes the process as it occurs when the vertebrate classes are considered, yet *adaptive branching* more accurately expresses what takes place in the orders and families, which do not radiate in all directions, nor always in straight lines, but in branches that often turn and change their direction.

Osborn applied his law mainly to the mammals, but it is equally true of other groups such as the reptiles, especially during the

ADAPTIVE RADIATION (*Teeth*)

(ADAPTED FROM OSBORN)



The adaptations appearing under each of these radii will be discussed in detail in this and subsequent chapters.

Mesozoic, before the mammals came to their own. The central or focal type is conceived as a short-limbed, ambulatory form, with five clawed digits upon the approximately equally developed feet. It was small and generalized in its feeding habits, insectivorous (that is, devouring insects, worms or such creatures) or omnivorous and therefore with simple short-crowned teeth.

The impelling causes of adaptive radiation are the need of food and the need of safety, and while the minor roads along which evolution is possible are many and devious, they all lead in four general directions: over the earth's surface where speed would become the great desideratum (cursorial), beneath the surface to the subterranean realm (fossorial), above the surface into the trees (scansorial), or finally into the air (volant) and into the water to become denizens, wholly or in part, of the aquatic realm. Subterranean life results in degenerative specialization, so that a return of fossorial creatures to the terrestrial habitat is rare, while the aquatic realm modifies its inhabitants so profoundly that there

is no known case of a return on the part of a lung-breathing form which has been adapted to aquatic life. These two roads—to the waters and the subterranean fastnesses—are one-way trails along which many go but none return.

Primary and Secondary Acquired Adaptations.—Adaptations are direct or primary if they lie in the original direction of adaptation, outward along any of the four radii (see page 247), as from terrestrial through scansorial to volant; or they may be reversed or secondary, when the return direction is indicated. While from the nature of its flying mechanism, which involves the hind limbs, it is, as we shall see in Chapter XXII, impossible to conceive of a secondarily flightless mammal such as the bat, nor are any such recorded; nevertheless there are many instances of flightless birds, which have reverted to their original environment. They were probably ground or sea birds, however, before flight was lost. There is thus a reversal of the *direction* of evolution, but this does not actually contradict the law of irreversibility of evolution, which says that an organ once lost can never be regained and that a specialized form can never again become generalized. A further example will make this clear. The marsupials are either all arboreal to-day or give evidence in their anatomy of arboreal descent. One striking arboreal feature is a grasping great toe or hallux on the hind feet (see Fig. 39,A). This, being off-

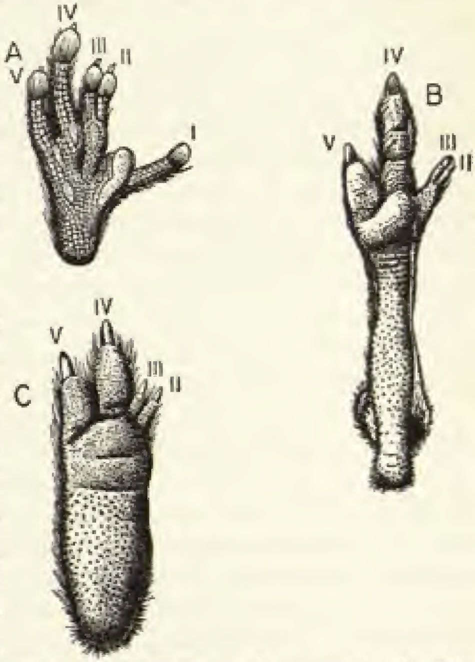


FIG. 39.—Hind feet of marsupials. A, opossum, *Marmosa pusilla*, with grasping hallux, arboreal; B, kangaroo, *Macropus dorsalis*, without hallux, digits II and III syndactyl, cursorial; C, tree kangaroo, *Dendrolagus ursinus*, without hallux, arboreal (secondarily). (After Bensley.)

set, opposes usually the fourth digit, thus forming an admirable prehensile organ whose grasp of a branch it is difficult to loosen. The terrestrial kangaroos, on the other hand, have become adapted in a wonderful way for speed over the earth's surface, and among other things have entirely lost this grasping hallux (see Fig. 39,B), as reduction of the lateral digits, much or little, invariably accompanies evolution for speed. There is, however, a tree kangaroo, *Dendrolagus*, which is very much at home in its arboreal retreat; having no grasping great toes, it has to rely upon its claws and broadened soles for security (see Fig. 39,C) and they are well suited to the task, although the hallux would undoubtedly be better. *Dendrolagus*, while arboreal, shows in the loss of this useful member a terrestrial ancestry, and back of that, in common with all marsupials, an arboreal one. Hence for it the course of adaptation has been reversed, but the reversal is one of function and not one of structure, for however useful the grasping hallux might be in the present environment, its loss during the terrestrial career of the ancestors is irrevocable. While the atrophied organ therefore is lost forever, its old-time function may be secondarily acquired by other organs should the need arise.

Other instances would be those of marine reptiles like the ichthyosaurs, or whales among mammals, both of which were derived indirectly from a fish ancestry, but which during the subsequent terrestrial life of their later progenitors lost the water-respiring gills. Perhaps the greatest menace to the safety of the modern whale is the necessity of rising to the surface to breathe, but the loss of gill-breathing is irrevocable and no organ apparently has been able to take its place (see Chapter XX). Primarily these forms were terrestrial animals, secondarily they have in many marvellous ways been adapted to the new environment, but owing to the law of irreversibility their adaptation apparently may never be perfected. Rodents are normally gnawing, herbivorous, terrestrial animals, certain ones being aquatic and fish-eating, the muskrat devouring both fish and fresh-water clams.

Local Adaptive Branching.—The law of adaptive radiation which has been cited refers to evolution on a broad scale and includes the entire mammalian or reptilian fauna of a continent. Local adaptive branching, on the other hand, is restricted to the differences arising within a group of closely related forms whose life habits are in the main similar. Africa supports to-day two

very distinct types of rhinoceros—the square-mouth or white and the pointed-lip or black rhino (see Fig. 40). With the square lip go long-crowned or hypsodont (Gr. ὕψι, on high, and ὀδούς, tooth) teeth, while the pointed lip is correlated with short-crowned or brachyodont (Gr. βραχύς, short) grinders. The differentiation is one therefore of feeding habits, the first largely grazing, the second browsing, and the local distribution of the two types is in harmony with this distinction in that the square-mouth rhino inhabits the open country, especially the broad grassy valleys between the tracts of brush south of the Zambesi River, while the pointed-lip species, on the other hand, is found in the wooded and watered districts from Abyssinia to Cape Colony. Geographically

FIG. 40.—African rhinoceroses. A, square-mouth or white rhinoceros, *Rhinoceros simus;* B, pointed-mouth or black rhinoceros, *R. bicornis.* (From British Museum Guide to Great Game Animals.)

therefore the range of the black rhinoceros includes that of the white, but is more extensive, as the species is far more common; locally the two habitats are distinct and have given rise to feeding and consequently structural differentiation. Similar instances are repeatedly met with, especially among prehistoric forms such as the horses. Differences, slight at first, will in the course of time be accentuated so that the ultimate descendants are very unlike each other. A specific instance, comparable to the African rhinoceros, is that of the American Miocene horses *Hypohippus* and *Merychippus.* The first had short-crowned, uncemented, browsing teeth and well developed lateral hoofs, forming a foot fitted for yielding ground like that of the forested areas. The second had complex, long-crowned, grazing teeth adapted to grasses, and

feet fitted for the hard prairie soil. The distinction between these two races may well have had its inception during late Oligocene time when differentiation of habitat was already established, but we cannot with our present evidence clearly separate the phyla until Lower Miocene at least (see Chapter XXXVI). Local adaptive branching therefore gives rise to different phyla of the same group of animals in a relatively small area.

Continental Adaptive Radiation, on the other hand, is on a broad scale and, as has been said, embraces the entire fauna of a given class (*i. e.*, Mammalia). Such radiations have appeared more than once, sometimes as repetitions of evolution within the same area, or again the radiations may be contemporaneous, but within the limits of distinct isolated continental masses.

Contemporaneous Radiations.—As we learned in the chapter on geographical distribution, the world's surface may be divided into three coequal but not coextensive realms: Arctogæa, Neogæa, and Notogæa, of which the first includes all of the northern hemisphere, and Africa; the second, South America; and the third, Australia. These three great realms have been the centers respectively of three remarkable adaptive radiations of mammals during Tertiary time, when all three were isolated each from the other in such a way as to prohibit absolutely for a long period all faunal interchange. This isolation is true of Australia to this day. Hence while the South American mammals have practically ceased to exist (see Chapter XXXVIII), Australia's fauna, except for certain overseas migrants introduced largely through human intervention, remains practically as it has been, composed of mammals of Mesozoic rather than of Tertiary type. Between Australia and Arctogæa there are some very remarkable parallelisms, for, upon a more limited scale, nature has nevertheless repeated herself, though not exactly, in the lesser continent. A comparison of the two radiations may be made.

In *Arctogæa* the central or focal type is represented in a general way by the Malayan insectivore, *Gymnura* (Fig. 41). This creature belongs to the hedgehog family, Erinaceidæ, but the more familiar European hedgehog, *Erinaceus*, is somewhat too specialized in its quill-like hairs and burrowing habits and consequent modification to serve as the focal type.

Along the cursorial radius we have in the dogs, especially the swift fox and the coyote, creatures of amazing speed although

digitigrade, that is, running upon the toes. Unguligrade or hoofed runners are best represented by the deer, the African and Mongolian antelope, but especially by the horse-like animal, the ghorkhar (*Equus onager*), which inhabits the Persian desert, an animal so swift that adults in good condition can neither be ridden down, unless by relays of horsemen, nor taken with greyhounds (Lydekker).

Arboreal forms are represented by the squirrels, some of which—the flying squirrels—have learned to launch themselves into the

FIG. 41.—The most primitive living representative of the Insectivora, *Gymnura*. (After Horsfield and Vigors.)

air and take long soaring leaps, supported by folds of skin between the limbs and the sides of the body, and hence have become semi-aërial. Truly volant or aërial forms are represented among mammals by the bats, which, however, belong to a different order than the flying squirrels, as they are directly out of the insectivorous stock, although no annectant forms are now alive. One remarkable insectivore, *Galeopithecus*, which will be described more in detail later, is a wonderful glider, and while not in the line of bat descent shows us quite clearly how such an adaptation could have arisen.

Aquatic-amphibious forms are represented by the *Potomogale* among insectivores, the muskrats and beaver among rodents, and the otters, but especially the seals, among carnivores; while the truly aquatic types are such as the porpoises and whales, which are apparently modified ancient carnivores, and the sea-cows (manatee, and dugong), which were derived from the ungulate stock.

Subterranean forms are the insectivorous shrews and moles and the rodent woodchucks, gophers, and mole-rats (*Bathyergus*). Of these the true moles and the golden moles (Chrysochloridæ) of the Cape of Good Hope, two entirely independent evolutions of mole-like forms, are the most extreme.

Notogæa.—The Australian mammals, as we have learned, are practically all marsupials or pouch-bearing mammals, whose young are brought forth at an extremely early stage of development, transferred to the pouch-covered nipples, and there nourished as "larvæ" until mature enough to stand the vicissitudes of ordinary

FIG. 42.—Opossum, *Didelphis marsupialis*, one of the most primitive living marsupials. (After Lydekker.)

animal childhood, when they are virtually reborn. There is no placenta, except for one or two rare vestiges (*Phascolarctos, Perameles*), and the young, being inadequately nourished compared with placental mammals, cannot stand competition with the latter even in their adult condition. Such was the stock with which Australia was inoculated, in the Mesozoic age and out of that stock, due to the immense period of isolation which has elapsed, there has arisen an adaptive radiation paralleling that of Arctogæa in many remarkable ways.

Perhaps the creature nearest the focal form among marsupials is the opossum (Fig. 42). The opossum is now an American form and therefore in its existing condition cannot represent the actual

ancestor, but it gives a good impression of what the Australian stem form was like. Opossums are, however, extremely old, persistently primitive forms, of which near relatives are found in Cretaceous rocks. They have survived contemporaneously with their diversified descendants. The opossum is arboreal, but it is quite probable that the marsupials had all passed through a tree-inhabiting stage before their great radiation began.

Cursorial adaptation in the marsupials is well shown in the Tasmanian wolf, *Thylacynus*, which is very dog-like in contour, development of limbs, and digital reduction. It is perhaps a little less extreme in its cursorial adaptation than the jackal (*Canis aureus*) for instance, as the distal segments of the limbs, whose relative lengthening is generally a speed requirement, are still proportionally short. *Thylacynus* clearly occupies the station of the wolves and dogs of Arctogæa, a fact which has caused its extinction when brought into competition with true canids (*i. e., Canis dingo*, see page 124). The herbivorous bandicoots and kangaroos are highly speedy and represent the ungulates of Arctogæa, the bandicoots (*Chæropus*) being quadrupeds whose hind foot has but a single dominant digit, although other vestigial ones are present. The kangaroos, on the other hand, are bipedal when running, with feet which are remarkably effective.

Arboreal marsupials are still numerous, the so-called "sugar squirrels" or phalangers being very similar to our squirrels in appearance, while the Arctogæan flying squirrels are represented with great fidelity by the Notogæan flying phalanger (*Petaurus sciureus*). A further extreme of arboreal adaptation is shown in the koala (*Phascolarctos cinereus*), slow-moving, tailless, with splendidly adapted hands and feet, the former having two fingers offset against the other three, and the latter the hallux against the other four, especially the fourth and fifth. In many ways the koala resembles the lemurs or half-apes of Arctogæa, especially such forms as the loris, *Nycticebus*.

No truly volant forms comparable to the bats exist in the Australian marsupial fauna, although placental bats are present, nor is there record of their having existed there during geologic time.

Aquatic types among marsupials are restricted to amphibious forms, truly aquatic types comparable to the Cetacea being unknown and improbable, for such would lack the isolation and security from competition so necessary to marsupial evolution.

Strangely enough, however, there is no recorded instance of even an amphibious marsupial in the existing Australian fauna, although South America possesses one, the water opossum (*Chironectes*), whose hind feet are webbed and whose general appearance reminds one of the muskrats, though of course, unlike the latter, it is exclusively carnivorous in its diet. It is highly improbable, however, that Australia has never possessed an amphibious marsupial.

Notogæa is not without its amphibious type, for the duck-bill or duck-mole (*Ornithorhynchus*) is a remarkable combination of burrowing and swimming animal, the projecting swimming membrane of the fore foot being folded back against the palm, exposing the powerful claws, when the creature wishes to dig. In its life habits the duck-bill is not unlike the muskrat, but the food differs, as it feeds upon various small water-animals, such as crustaceans, insects and their larvæ, snails and worms, which are dug out of the soft mud by the tender muzzle. *Echidna*, an ally of *Ornithorhynchus*, while having a pouch for the protection of the newly hatched young, is not a member of the order Marsupialia but of the yet more primitive Monotremata—the egg-laying mammals—which while strictly Notogæan in their existing distribution, are nevertheless not of the present Australian adaptive radiation, as that implies a common, *i. e.*, marsupial, ancestry, but are survivors of an earlier evolution.

Fossorial Notogæan animals are admirably represented by the marsupial "mole," *Notoryctes typhlops*, a recently discovered type, which bears a remarkably close resemblance in its molar teeth, external form, and mode of life to the South African golden moles (Chrysochloridæ) of which we have spoken. But they cannot be related, for *Chrysochloris* is a placental insectivore and *Notoryctes* a marsupial. They therefore represent one of the most interesting cases of convergent evolution of which we have knowledge.

Thus it will be seen that the Australian adaptive radiation practically coincides with that of Arctogæa, almost every animal in the former assemblage having some approximate equivalent in the latter. The reverse, on the other hand, does not hold true, for the Arctogæan realm is relatively so vast and its range of habitat conditions so much greater, that its fauna is proportionately more extensive and varied.

The ancient fauna of Notogæa has but a dubious future, for the

artificial introduction of several placental mammals has already made serious inroads into the integrity of the marsupial ranks, the dingo having driven the Tasmanian wolf from the Australian mainland while the rabbits and sheep, through their destruction of the food supply, have reduced the marsupial herbivorous population by cutting off their means of subsistence. To this must be added the destruction of marsupials by mankind, for the hides, both for furs and leather, are commercially known as opossum and kangaroo respectively. It is quite probable that, with few exceptions, this ancient radiation is doomed to speedy extinction.

Successive Radiations in Time.—There have been three successive radiations among mammals of which the first, however, that during the *Mesozoic*, was comparatively unimportant because of the terrestrial dominance of the dinosaurs and other reptiles. During this radiation the known mammals were all small, although differentiated into three or four phyla from the standpoint of their dentition and implied feeding habits. Thus some were insectivorous, some perhaps more distinctly carnivorous, and some herbivorous, possibly fruit- or nut-eating (seed-eating?).

It was not until the great reptilian extinctions at the close of the Cretaceous that the mammals really had their opportunity, at least in the known fossil-bearing regions; and with the vacating of the terrestrial realm by the huge cold-blooded brutes, the higher creation began its deployment in the known areas. Paleontologists soon find records of carnivorous forms (creodonts) of various sorts, swift cursorial ungulates (condylarths), and slow-moving, grotesquely armed types (amblypods). There were also sloth-like forms (tæniodonts) and probably ancestral marsupials. Of all of these so-called archaic mammals, but few survived the Eocene; some were sooner or later rendered extinct through competition with invaders of the third or Tertiary radiation, others may have evolved into certain of the higher types, yet others, driven southward into Neogæa and Notogæa, may have formed the stock of part at least of their subsequent faunas when isolation closed the door upon later invaders. These archaic mammals, their adaptations and their defects will be discussed more at length in Chapter XXXII.

The *Tertiary* radiation was the great Arctogæan radiation of modernized mammals, so called because their descendants still exist; at all events no higher group has appeared, and the story of mammalian evolution in this world, owing to the present domi-

nance of man, is virtually over. Whence the progenitors of the modernized mammals came we have no positive knowledge, but circumstantial evidence points to boreal Holarctica—the circumpolar lands of the northern hemisphere—as their pristine home. For in the Cretaceous and early Eocene indications point to a warm climate and abundant forestation in the north, ideal conditions for the well-being of the nodal type and its immediate derivatives. Increasing cold in the northland drove forests and their fauna south down the three great continental axes (see map, Fig. 254) so that we find creatures of much the same sort, such as the ancestral horses, appearing synchronously in the Old World and in the New. Early in the Eocene their deployment was well under way, the Oligocene saw certain lines already approaching racial death and others wondrously varied, while during the Miocene the culmination was reached and never before nor since was there so great a mammalian florescence. By the Pliocene they had begun to wane. The mammals of to-day, including man himself, are the remnant of this Tertiary radiation.

Tooth Radiation.—The mammals are, with few exceptions (Cetacea, anteaters, etc.), characterized by a heterodont (ἕτερος, different, and ὀδούς, tooth) dentition, that is, the teeth, in contrast to those of most reptiles, for instance, are differentiated into several sorts with, as a rule, very distinct functions. Those in the front of the mouth, the incisors, are mainly prehensile, the canines grasping, tearing, or for defense or offense, the premolars sometimes shearing, or, like the molars, grinding teeth. The last mentioned molars and premolars show the greatest structural modification to meet their owner's requirements, the incisors and canines being more conservative, as their use shows less variation in the different orders. See Fig. 43.

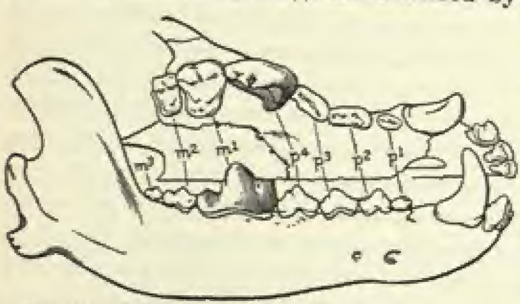


FIG. 43.—Upper and lower teeth of the wolf, *Canis lupus*, showing the carnassial or flesh-cutting teeth, shaded. (The fourth upper premolar and first lower molar.) m^1-m^3, molars 1 to 3; p^1-p^4, premolars 1–4. (After Matthew.)

The *insectivorous type,* those of the stem form, are low-crowned, simple, with few cusps, generally sharp-pointed and suitable for crushing feeble prey. With the *carnivores,* the cheek teeth become high-crowned, trenchant, shearing structures, and the jaws have little or no lateral play. This reaches its highest specialization in the cats (see Chapter XXXIII), wherein the true grinding teeth are almost entirely wanting. In the dogs, with a less exclusive diet, more of the grinders are retained, although the shearing teeth are well developed, while in the bears, carnivores with a strong tendency toward an herbivorous diet (omnivorous), the cheek teeth are broad-crowned, tuberculate grinding organs, and shearing teeth are wanting. Carrion-feeding forms have, as a rule, blunter teeth, while in fish-eating creatures like the seals the teeth have become secondarily simplified and are all prehensile. The toothed whales (Odontoceti) have lost their tooth differentiation and the teeth are practically all alike—simple, slightly recurved, grasping cones. The teeth are sometimes absent in the upper jaw (sperm whale, *Physeter,* in which, while germs of upper teeth are present, they are apparently functionless), and in the whalebone whales (Mystaceti) they are entirely absent, except for functionless vestiges in the unborn young, and their place is taken by the curious baleen or whalebone which hangs from the palate and by means of which small molluscs and crustaceans are strained out of the water to serve for food (see Chapter XXXIV).

Herbivorous forms have the incisors fitted for seizing and cutting the vegetation. In the ruminants, however, they are absent in the upper jaw, the lower incisors biting against a horny pad. Canine teeth are of little importance to the herbivore unless they are used for defense (musk deer), or as in the swine for uprooting the vegetation upon which they feed. The grinders vary amazingly in the pattern of the cusps and crests borne upon the crown but in general may be divided into short-crowned, brachyodont teeth fitted for succulent leaves and twigs; or long-crowned, hypsodont teeth whose great length and complex structure are adapted to meet the wear imposed by the harsh grasses and other vegetation which form the staple of a grazing animal. Perhaps the greatest degree of perfection has been reached by the modern horse (*Equus,* see Fig. 216) along one line of descent and the elephant, more especially the extinct woolly mammoth (*Mammonteus primigenius,* compare Fig. 215) along another.

As we have seen, a carnivore like the bear may become adapted to an all-round diet and hence be *omnivorous*, but the term is best applied to a direct line of evolution from the insectivorous stock, such as the primates, and especially mankind. Here the incisors and canines show little distinction and the cheek teeth are very simple and primitive, with bicuspid premolars and molars with few (four or five) low cusps.

The *myrmecophagous type* represents the height of specialization, for in its extreme development the teeth have utterly disappeared, the jaws are reduced, the mouth is incapable of opening except at the extreme anterior end and has become tubular, with a highly extensile and prehensile tongue. This organ is provided with an adhesive substance and when thrust into an ant-hill and withdrawn brings away great numbers of the unfortunate insects, which are swallowed without mastication. As a special adaptation to such rather insurgent prey, the interior nostrils are carried far backward so as to be in direct communication with the windpipe to prevent any of the creatures from wandering the wrong way. An analogous adaptation is seen in the marsupials to avoid suffocation when the milk is forced into the mouth of the feeble young by the mother's muscles, and in the whales and again in the crocodiles, both of which devour their prey under the water and would run the risk of strangulation were it not for this device.

Summary.—We have thus emphasized the wonderful plasticity of living beings, which, in their efforts to find food and safety, become adapted in the course of time to all possible conditions of life—earth, air, water, the most salubrious as well as the most forbidding wastes; and have shown that these adaptations are chiefly concerned with those parts most closely in contact with the environment—the feet for safety and the teeth for food. The soft parts are generally more conservative and while feet and teeth undergo their marvellous changes, internal organs, except such as are again directly concerned with diet or locomotion, may remain comparatively unaltered. We find that nature does repeat herself, but never exactly, nevertheless some remarkable convergences of unrelated animals are recorded. The final truth is that a highly adapted or specialized form becomes, as it were, stereotyped and incapable of radical change, and with altering conditions may succumb where a less specialized and therefore more plastic race, meeting the changed requirements, survives.

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CHAPTER XIX

CURSORIAL AND FOSSORIAL ADAPTATION

Cursorial Adaptation

We have already discussed various means whereby creatures compete with each other for the two prime requisites of existence—food and safety. These took the form of coloration, of mimicry, of stealth, of parasitism, or of bodily prowess. Now we would speak of forms which live in the open, of the pursuer and the pursued, for while such creatures do not perhaps constitute a very large proportion of the animal kingdom, as do the parasites for instance, they are nevertheless of great importance, and the evolution of remotely related types has given rise to some remarkable instances of convergent evolution.

Speed adaptation has been developed in a very wonderful way in terrestrial (cursorial) types, in aquatic, and finally in aërial forms. Of these we will first discuss the terrestrial.

Vertebrates Showing Speed Adaptation.—The following is a list of vertebrates which show this adaptation for speed:

Class Reptilia. Reptiles

Order Squamata. Lizards and snakes.
 Especially certain of the Agamidæ. *Chlamydosaurus*, the frilled lizard of Australia. Numerous others, especially desert-inhabiting forms.

Dinosaurs (see Chapters XXX and XXXI).
 Order Saurischia. Carnivorous and amphibious dinosaurs.
 Most of the carnivorous dinosaurs, especially the smaller, more agile forms: *Podokesaurus*, *Hallopus*, *Cœlurus*, *Compsognathus*, *Ornithomimus* and *Ornitholestes*.
 Order Ornithischia. Herbivorous beaked dinosaurs.
 Nanosaurus and the Camptosauridæ.

Class Aves. Birds

Division Ratitæ. Flightless cursorial birds.
 Especially emus, cassowaries, ostriches, and rheas, and probably the extinct Dinornithes, the moas of New Zealand.

Division Carinatæ. Flying birds.
Of these few are adapted for speed except perhaps the rails, one of which (*Aptornis*) is flightless.
Certain of the Limicolæ, plovers, oyster-catchers, etc., are also speedy for short distances.

CLASS MAMMALIA. MAMMALS

Order Marsupialia.
Dasyuridæ, especially *Thylacynus*, the dog-like Tasmanian "wolf."
Peramelidæ, the bandicoots.
Macropodidæ, the kangaroos.
Order Rodentia.
Leporidæ. Hares and rabbits.
Caviidæ. Cavies.
Dipodidæ. Jerboas.
Order Carnivora.
Canidæ. Dogs.
Felidæ. Cats. Especially *Acinonyx*, the cheetah or hunting leopard.
Cohort Ungulata.
Order Perissodactyla.
Hyracodontidæ. Extinct cursorial rhinoceroses.
Equidæ. Horses, living and extinct (see Chapter XXXVI).
Order Artiodactyla.
Protoceratidæ. Extinct.
Antilocapridæ. American prong-horn antelope, *Antilocapra*.
Cervidæ. Deer.
Bovidæ. Especially the African antelopes.
Giraffidæ. Giraffe and okapi.
Tylopoda. Camels (see Chapter XXXVII).
Order Litopterna. South American ungulates (see Chapter XXXVIII).
Especially the Proterotheriidæ, the extinct "pseudo-horses."

Body Contour.—All speedy animals, whether terrestrial, aquatic, or aërial, have the body moulded externally in such a way as to offer the least resistance to the medium through which they pass. Owing to the greater resistance of water, this is especially true of the aquatic, nevertheless a speedy cursorial type also shows it, though not always as well when at rest as it does when in action. A race-horse with head and neck extended, ears thrown back, and every tense muscle of its wonderful body working with machine-like precision, shows the beautiful contour of a perfectly adapted mechanism. The body spindle-shape, of stream-line contour, the lines extended into the neck and head without a break in their even curves—all are calculated for swift passage through the air with a minimum of resistance.

Mechanism

Loss of General Utility.—The propelling organs in cursorial forms are the limbs exclusively, so that, aside from the resistance-lessening contour, this adaptation concerns itself chiefly with their modification, of which the first is the loss of general utility. This is especially true of the hind limbs, because they are the more efficient drivers and therefore, especially in forms whose adaptation has not gone very far, are likely to be somewhat in advance of the fore limbs in the degree of their evolution. For this several reasons may be assigned: (1) The extended hands pull the body forward in running; (2) the fore part of the body is usually heavier than the hind part and requires larger limbs to support and propel it; (3) running is a sort of leaping on all fours, and the hands are larger and wider to take the impact when the animal falls forward; finally (4) the fore limbs, being nearer the mouth and hence perhaps somewhat concerned in food-getting, are the last to lose their general utility. Two notable instances of this accelerated evolution of the hind limbs over the fore are the early four-toed horses of the Eocene (Hyracotheres, see Chapter XXXVI) in which, while the hand still retains its four digits, the foot has but three. It is not until Oligocene time that the additional finger is lost and the evolution of both limbs becomes parallel. In another Oligocene form, *Protoceras*, a curious artiodactyl with remarkable excrescences upon the skull and dagger-like canine teeth, the hand is four-toed while the foot has but two.

Change in Foot Posture.—The primitive terrestrial foot is plantigrade (Lat. *planta*, sole, and *gradi*, to walk), which means that the entire palm or sole rests on the ground, neither wrist nor ankle being raised. Almost the first step in speed adaptation is the lengthening of the limb and this may be accomplished without the actual elongation of a bone, merely by rising upon the toes. While the bear, raccoon, and the primates such as the baboons and man are plantigrade, probably secondarily so, a large proportion of modernized mammals have become digitigrade (Lat. *digitus*, finger, toe), walking or running upon the digits themselves, with the bones of the wrist (carpal) and ankle (tarsal), the upper ends of the palm (metacarpal) and the sole bones (metatarsal) clear of the ground. Some of the speediest of animals—dinosaurs, birds, dogs, all mammals in fact but the ungulates—have merely per-

fected the digitigrade gait, developing special sole-pads for the absorption of the shock of impact, and have never gone beyond it. The ungulates or hoofed animals, on the other hand, walk on the modified nail or hoof (unguligrade, Lat. *ungula*, hoof), the distal toe-bones (unguals) being depressed or flattened and not, with rare exceptions, compressed or claw-like. The hoof has reached the highest degree of perfection in the horses; in other related but non-cursorial types like the rhinoceros the hoofs bear little of the weight, as a broad cushion-like pad serves instead (see Fig. 45).

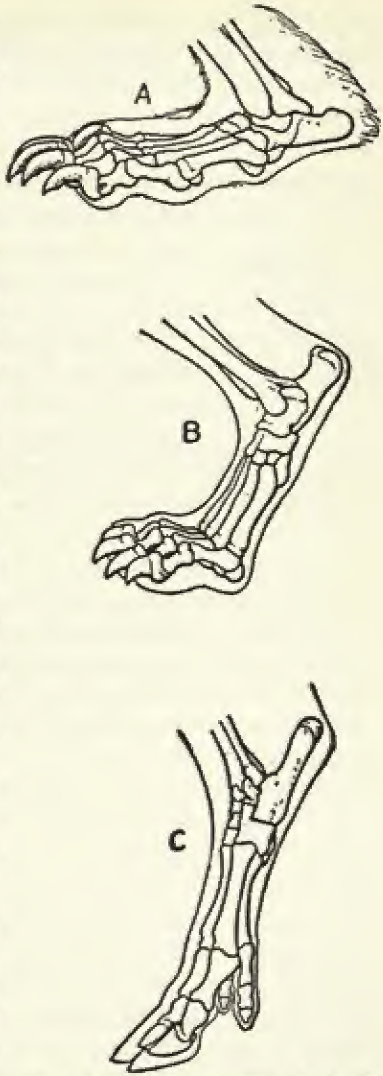

FIG. 44.—Foot postures. A, plantigrade, bear; B, digitigrade, hyæna; C, unguligrade, pig. (After Pander and D'Alton.)

Ungulate animals show all gradations from the semi-plantigrade condition of the slower forms to the high, stilted hoofs of certain of the African antelope, notably the klipspringer (*Oreotragus saltator*). A truly unguligrade condition has never been attained among reptiles, although certain beaked dinosaurs had depressed instead of claw-like unguals. *Triceratops* and *Stegosaurus* were certainly far from speedy; hadrosaurs, on the other hand, which also bore this type of ungual, were bipedal and doubtless possessed a fair measure of speed when well under way, though little celerity of movement is indicated.

Certain ungulates like the modern camels have become secondarily digitigrade, the foot having retrogressed as an adaptation to

the yielding desert sands (see page 608). This is not accompanied, however, by any material loss of speed, as the camels are among the most remarkable travelers of all terrestrial forms.

Loss of Digits.—Plantigrade animals are generally five-toed; there are of course exceptions, but the elevation of the heel or wrist generally carries with it digital reduction, digitigrade animals becoming four-toed, unguligrade four-, three-, two-, or even one-toed (see page 585), two toes in the artiodactyls and one in the perissodactyls being the irreducible minimum.

FIG. 45. — Rhinoceros foot, sectioned to show the supporting pad. (After Osborn.)

The frilled lizard of Australia, *Chlamydosaurus*, is five-toed but the lateral toes are shorter than the median ones, which is almost universally true except in aquatic types such as the seal and otter. Hence when *Chlamydosaurus* runs on its hind feet, as it does when startled, the outer and inner toes are raised off the ground and the animal makes a three-toed track. If this were the habitual gait of the creature, the lateral digits would be rendered practically useless and would follow the course of all useless organs and become reduced, whatever the philosophical explanation of the mean whereby this is accomplished.

Environment as well as speed adaptation has its influence in determining digital reduction, for it will be accelerated if the ground is hard, as in the prairie-evolved horse with but one remaining digit, or the prong-horn antelope of similar environment with two. On the other hand, the Miocene forest horse, *Hypohippus*, retained the lateral toes as functional organs just as the reindeer and caribou (*Rangifer*) have to-day, as an adaptation to a yielding footing, while contemporary relatives had in each instance evolved much farther along the line of digital reduction.

Concurrent with the loss of digits, especially if the foot be lengthening after the manner to be described below, comes a compacting of the bones of the palm and sole (metapodials) and often this is carried so far as to give rise to actual fusion of these elements into a "cannon-bone." The dinosaurs, with one doubtful exception, never attained an actual fusion, although in many respects, especially in *Ornithomimus* of the Cretaceous, the foot is very bird-like. The birds, on the other hand, always show a fusion of the metatarsals. Among mammals the carnivores do not form

a cannon-bone nor does the marsupial wolf; but all of the speed-adapted ungulates do. Ancient ungulates, however, had the metatarsals separate, and we can often witness the fusion in fossil series (camels, etc.) when the proper degree of speed adaptation has been reached. Among rodents, the jerboa (see Fig. 48), a three-toed bipedal form, has a foot and metatarsus so wonderfully bird-like that one almost has to count the phalanges of the digits to be sure he has a mammal before him.

Reduction of Fibula and Ulna.—The fore arm and shin, that is, the second segment from the body, have each typically two bones: in the arm, the radius and ulna, and in the leg, the tibia and fibula. These are both developed in slow-moving forms or where the fore limb still has considerable general utility, especially if the rotation of the hand on the arm is retained. On the other hand, cursorial forms, especially if the limbs are exclusively locomotor, tend to reduce the ulna of the arm, the proximal end only being present in extreme cases to form the elbow joint. They also lose the fibula of the leg, which may be reduced to the merest vestige.

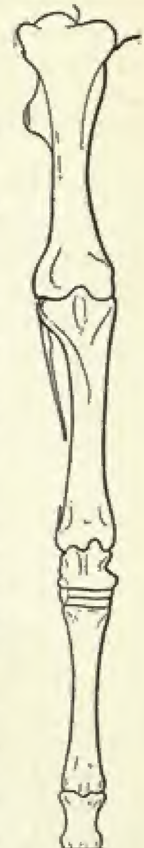

Fig. 46.—Hind limb of horse, *Equus caballus*, to show pulley-like joints for the restriction of movement to one plane.

Loss of Universal Movement.—The entire motion of the limbs becomes pendulum-like, that is, restricted to movement in but one plane, the exception being at the hip and shoulder, where universal movement is still retained through the development of a ball-and-socket articulation. The necessity for this is apparent, first to avoid interference between fore and hind feet when running, since a dog, for instance, at top speed brings his hind feet well in advance and outside of the fore. A second need is that of lying down and rising again, which would be practically impossible were the movement at hip and shoulder restricted to the fore-and-aft plane. With the other articulations, those of ankle and wrist, knee and elbow, and between the digits, the tendency is toward rigid limitation of movement in

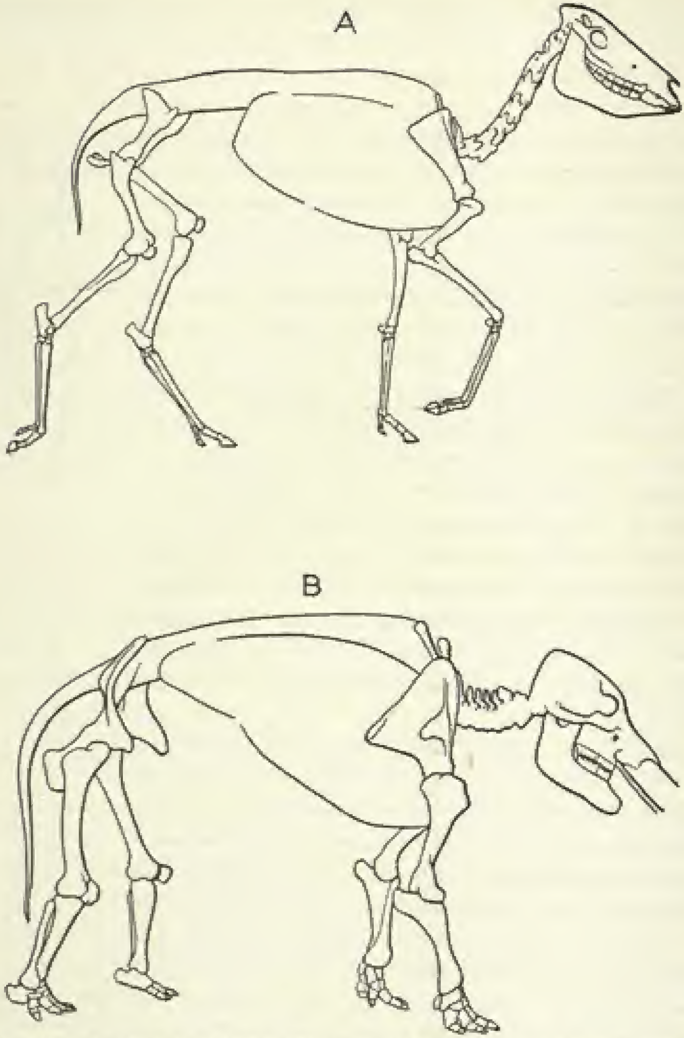

Fig. 47.—A, three-toed horse, *Hipparion* (*Neohipparion*), showing cursorial adaptation for run or gallop; B, mastodon, *M. americanus*, showing graviportal (rectigrade) adaptation for walk or amble. (After W. K. Gregory.)

unguligrade, less so in digitigrade forms. This is accomplished by the development of tongue and groove joints such as were discussed under kinetogenesis (see Chapter XII). These are very perfectly shown in the hind limb of a modern horse, as well as at the elbow joint (see Fig. 46), forming in each instance an articulation permitting movement through a wide arc in one plane of space and none whatever in any other. These joints, while they may be broken, cannot be dislocated.

The limbs are compound levers, for not only is there motion of the limb as a whole but also between its component parts. The lengths of each of the several segments bear definite relations to the speeds developed and also to the loads they have to carry. Those forms which, like the elephant, are mighty of frame, have a type of limb which is in marked contrast to that of a horse. To the former type has been applied the term graviportal (*i. e.*, weight-carrying), to the latter cursorial, although both are adapted to increase their owner's traveling powers. In the graviportal type such as the mastodon, the foot is short and the thigh and shin relatively long, whereas in a cursorial form the foot elongates and the thigh is conservative (see Fig. 47). This may be shown by a comparison of ratios between the middle metatarsal and the femur, thus:

Ratio: $\frac{\text{Length of metatarsal III}}{\text{Length of femur}}$

Graviportal		Subcursorial		Cursorial	
Uintatherium	.10	Eohippus	.50	Equus	.78
Mastodon	.11	Tragulus	.56	Antelope	1.00
Elephas	.13	Mesohippus	.57	Odocoileus *	1.00

* Virginia deer.

Lengthening of Limbs.—The lengthening of the limbs in cursorial types is usually thus accomplished by a growth of the distal segments only, the foot and shin and hand and fore arm increasing, but rarely the thigh or upper arm. This increase is therefore both actual and relative. This is well shown in comparing the limb of a horse with that of a man (see Pl. IV), for while the human thigh may actually exceed the length of that of the horse, the horse's foot, which is measured from the end of the hoof to the hock, the

equivalent of the human heel, may be two and a half times that of the man.

This lengthening of the distal segments, which is for the purpose of increasing the length of stride, would be of little avail were the muscles not concentrated at the proximal end of the limb, their power being transmitted by long slender tendons to the lower leg and foot. One effect of this may be best understood by comparing the limb with a pendulum. The length of the pendulum determines the scope of swing, but the position of its center of gravity controls its speed or rate of beat. To accelerate the beat, therefore, the bob is moved upward, to retard it, it is moved downward, the arc of pendular motion remaining constant. This concentration of the muscles at the proximal end of the limbs has the same effect as raising the pendulum bob, and by this device—long slender limb and high but powerful muscles—the maximum length of stride and speed of movement are obtained. While this may well be an important reason for the concentration of muscle, the parallel with the pendulum is not exact, for the opposing muscles not only serve to initiate the swing but also to damp it. Perhaps the chief reason, therefore, is that by raising the insertion points of the thigh-muscles focussing around the knee, the *angles of insertion* of many muscles are increased and this gives higher propulsive components, *across* the shaft of the femur; at the same time the muscles are shortened and made thicker, which increases their power and speed of contraction. It can readily be seen that a limit may be reached beyond which bone will not stand the strain to which it would be subjected, although bone is a wonderfully efficient material. Hence one would expect to find the greatest speed developed on the part of creatures of small to moderate size—the antelope of Africa or horses like the wild ass of Persia (*Equus onager*) the speed of which has been mentioned (see page 253) and which reaches a stature of but $11\frac{1}{2}$ hands. The Mongolian wild ass or kiang (*Equus kiang*), according to Roy Chapman Andrews, who chased one for 29 miles in a motor car, averaged 30 miles an hour for the first 16 miles and then when it began to slow down, still ran four more miles at a speed of 20 miles an hour. The modern race-horse is relatively small compared with some other breeds, and the limit of weight, size, and speed consistent with safety seems to have been approximately reached.

Ratios.—Lengthening of limbs also implies, at any rate in a quadruped, the concurrent lengthening of neck and skull in order that the animal may readily reach the ground for food and drink. Hence the various parts of an animal's frame bear definite ratios to one another and this may also extend to individual bone proportions, a definite "speed index" being recognizable. This makes it possible through the law of correlation to gain some insight into the habits of extinct and little-known forms through the study of comparatively fragmentary remains.

Bipedality

A two-footed mode of progression as an adaptation to speed has been repeatedly evolved among vertebrates, as follows:

Reptiles:
- Lizards, several occasionally bipedal.
- Dinosaurs, two evolutions.[1]

Birds:
- One evolution.

Mammals:
- Marsupials, one evolution.
- Rodents, three evolutions.[2]

In all, eight or more times.

The erect posture of man was probably not originally a speed adaptation, nevertheless speed has always been a vital factor in human evolution, in all offensive and defensive operations. The human foot, which was originally a climbing structure, has been readapted for bipedal walking and running. The long thigh and shin of modernized man increase the stride materially in contrast to those of the gorilla and chimpanzee. The Neanderthal man (see Chapter XL) had short stocky limbs as compared with the existing species, but doubtless could outrun any of the anthropoid apes.

Reduction of Fore Limbs.—In bipedal creatures the hind limbs form the exclusive means of *rapid* propulsion, hence all of the cursorial adaptations which have been mentioned apply solely to them. The fore limbs, on the other hand, retain their generalized character, as their sole use is for resting (kangaroo, herbivorous dinosaur)

[1] Assuming that the so-called dinosaurs are diphyletic (see Chapter XXX): Ornithischia, Saurischia.

[2] Heteromyidæ, Dipodidæ, Muridæ.

or for slow locomotion while feeding. They often serve as very efficient organs of prehension. Because of the marked division of labor between the limbs, disparity of size soon arises and, as cursorial adaptation is perfected, the fore limbs become smaller and smaller in proportion until at length, as in the ultimate carnivorous dinosaurs (see Chapter XXX, Fig. 147), they are so absurdly reduced that it is difficult to conjecture their use.

Counterpoise.—Some sort of counterpoise is always necessary in a semi-erect biped and the tail usually assumes this function. In the kangaroo and in the dinosaurs it is a powerful organ and serves as a prop, like a third limb, when the creature rests without coming down on all fours. The tail may be comparatively short and heavy in larger forms or extremely long and slender in more lightly built creatures, on the principle that an ounce at the end of a sixteen-inch lever is as effective as a pound on one but an inch in length. Many dinosaurs and bipedal lizards have a long, attenuated tail; this is especially true of the dinosaur *Podokesaurus* (Fig. 145), a Triassic form from the Connecticut valley, and of the Australian frilled lizard *Chlamydosaurus*. Among mammals the kangaroos have a relatively short, heavy tail; the jerboa on the other hand has a very long one terminating in a tuft of hair, which through its resistance to the air adds effect to the counterpoise.

No existing birds have a long tail, that is, as regards the actual tail itself, although the feathers may be long. These, as in the pheasants, may subserve a balancing function. The true cursorial birds, Ratitæ, are practically tailless, but maintain their balance with ease, the head and neck sufficing. The ostrich raises its wings as an aid in running, but with the practically wingless cassowary or the emu the head and neck alone must serve.

Shortening of Neck.—In bipedal mammals there is a tendency toward reduction in the length of the neck, especially in the rodents such as the jerboa (Fig. 48), in which cursorial adaptation is extreme and there is a remarkable cervical reduction associated with the shortened skull. There is of course no diminution in the number of neck vertebræ, for the number, seven, is with two or three exceptions (sloths and manatee) constant among mammals; but the vertebræ themselves are shortened and tend to coalesce into a rigid mass of bone. Thus in the rodent *Pedetes* cervicals 2 and 3 are so closely articulated as to eliminate motion, in *Perodipus*

the axis (2d cervical) and next two vertebræ are fused, while in *Dipus* (jerboa) all of the cervicals except the atlas (1st cervical) are coössified as in the whales. As we shall see, the shortening of

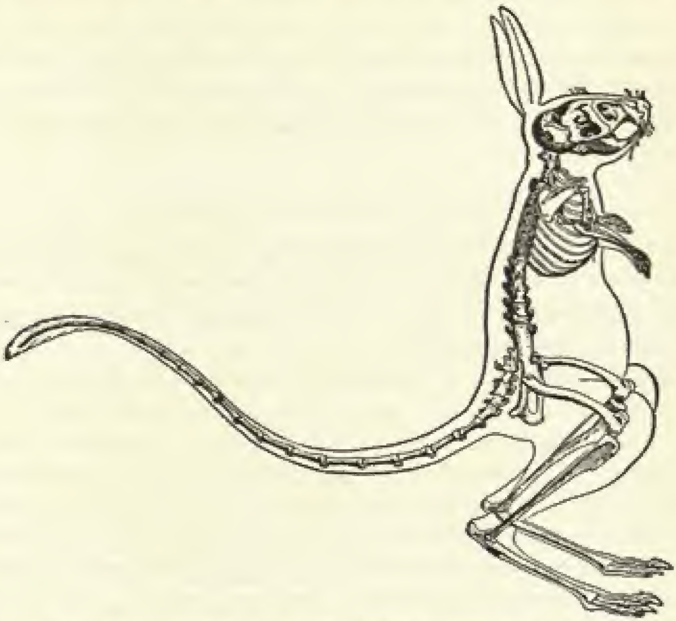

FIG. 48.—Skeleton of jerboa. (After Pander and D'Alton.)

the neck may be also an aquatic adaptation, since it occurs in the whales and sirenians (sea-cows).

Mental Precocity

Animals which depend upon speed for safety, as do the ungulates or the whales, cannot have helpless young. Such must either be brought forth in some secluded den or carried about by the mother. Carnivores and rodents have very feeble young, but they are kept hidden until able to shift for themselves. The kangaroo, on the other hand, must carry her offspring with her and this undoubtedly proves a very heavy handicap to the race when competition with higher forms prevails, for the destruction of the mother means that of the young as well. With all other forms which depend upon speed for safety, the young animal must be able to keep up with the herd almost at once. Hence there is no period of helpless in-

fancy, but the new-born deer or horse or camel, with its grotesquely long limbs, has the relative mental alertness of a very much older dog or rat, although the ultimate mental attainments of the ungulate may not be so great. As an illustration of precocity, Andrews describes an experience with a ten-day-old baby antelope. For four miles he seldom went slower than 25 miles per hour and for five more miles he averaged 15 miles per hour. He circled too quickly for the car in fact, which had to average about 40 miles to overtake him.

Significance of Cursorial Adaptation

Not only does speed adaptation give rise to some of nature's most beautiful and perfect machines, but it seems to have a much deeper meaning which has been summarized by Broom. He is speaking of Permian reptiles:

"The African, or more preferably the South Atlantic type, is chiefly remarkable for the great development of the limbs. . . . What may have been the cause we can not at present tell, but it was a most fortunate thing for the world. It was the lengthened limb that gave the start to the mammals. When the Therapsidan [mammal-like reptile] took to walking with its feet underneath and the body off the ground it first became possible for it to become a warm-blooded animal. All the characters that distinguish a mammal from a reptile are the result of increased activity—the soft flexible skin with hair, the more freely movable jaws, the perfect four-chambered heart, and the warm blood. It is further singularly interesting to note that the only other warm-blooded animals, the birds, arose in a similar fashion from a different reptilian group. A primitive sort of dinosaur took to walking on its hind legs, and the greatly increased activity possible resulted in the development of birds. Birds were reptiles that became active on their hind legs, mammals are reptiles that acquired activity through the development of all four."

Back of all this lay the impelling natural cause. The earliest known mammals are late Triassic, the first recorded bird Middle Jurassic; the inference that both stocks arose in Permian time is justifiable from the degree of evolution which each class had attained by the time the actual record of their existence begins. Schuchert tells us that early in the Permian the climate of the lands seems everywhere to have been arid or semi-arid and that this

condition lasted into Jurassic time. One characteristic of desert animals of to-day—the lizards, birds, gazelle, Persian ass—is *speed*, for the creature must fare widely for food and drink if he would fare well. Again we are told that during the Permian there was a period of extensive glaciation with a severity of climate, especially in the southern land masses, as great as, if not greater than, the polar one of Quaternary time, although, like the latter, the Permian glacial period had warmer interglacial intervals as well. The incentive for speed already given, rendering the development of warm blood possible, the devastating cold would soon place a premium upon such as did develop it and eliminate those which did not. From this fortunate relation of cause and effect might well have arisen on the one hand the primal mammal, making human evolution possible, and on the other hand the ancestral bird.

Fossorial Adaptation

Classification

Bionomic.—Fossorial types may be classified bionomically in a manner which denotes the degree of their adaptation to subterranean life. Thus there are, first, those whose habitation is above ground but which dig for their food. There are several such, like the swine and the elephant, but aside from the mere digging mechanism—snout, tusks, etc.—there is but little fossorial adaptation to be noted. Nevertheless, such as it is, it may have a far-reaching secondary effect upon correlated organs. Thus the entire modification of the skull, jaws, and trunk, besides the tusks, of the elephant—structures which sum up almost all of the recorded evolutionary change of the most remarkable of beasts—are either directly or indirectly the result of fossorial habit (see Chapter XXXV).

Secondarily, there are those creatures which dig for retreat and which show still greater modification, especially in the body and limbs; but those whose food is above ground are not so profoundly modified as those whose food also is found below. The latter, the wholly fossorial, exhibit the extreme of adaptation which is to be discussed.

Zoölogic.—Zoölogically, the partially and wholly fossorial animals are the lowly, more primitive and defenseless or unambitious members of their respective phyla. They include representatives

of every great vertebrate class except the fishes, but the appended approximate summary is based almost entirely upon existing forms.

CLASS AMPHIBIA

Cæcilians.

CLASS REPTILIA

Sphenodon
Uromastix.
Legless lizards.
Desert snakes.

CLASS AVES

Burrowing owl.
"Starlet" sp., of Mingan Islands.
Cliff swallow.

CLASS MAMMALIA

(All wholly fossorial mammals are primitive, small, plantigrade, pentadactyl, with moderate to large claws, and relatively defenseless.)

Order Monotremata. Entire order.
Order Marsupialia.
- Wombat (*Phascolomys*).
- Dasyure (*Dasyurus*).
- Kangaroo-rat (*Bettongia*).
- Pig-footed bandicoot (*Chæropus*).
- Marsupial mole (*Notoryctes*).

Order Edentata.
- Armadillos.
- Aardvark (*Orycteropus*).

Order Insectivora.
- Common moles (*Talpa, Condylura*).
- Golden mole (*Chrysochloris*).
- Shrew-mole (*Scalopus*).
- Water-shrew (*Crossopus*).
- Desman (*Mygale*).
- Hedgehog (*Erinaceus*).
- *Oryzorycles.*

Order Rodentia.
- Hares (*Lepus*).
- Ground-squirrels (*Spermophilus*).
- Prairie-dog (*Cynomys*).
- Woodchuck (*Arctomys*).
- Pocket-gopher (Geomyidæ).
- Mole-rats and bamboo-rat (Spalacidæ).
- Octodontidæ.
- Paca (*Cœlogenys*).
- Viscacha (*Lagostomus*).
- Bathyergidæ.
- Siphneinæ.

Order Carnivora (retreat only).
  Otter (*Lutra*).
  Ratel (*Mellivora*).
  Javanese skunk (*Mydaus*).
  American badger (*Taxidea*).
Cohort Ungulata.
  Few dig for food: swine, elephants, mastodons.

Modifications

Body Contour.—The density of the medium through which the burrowing form must penetrate necessitates a spindle or fusiform shape, not so beautifully modelled as in swift aquatic types, but such as will nevertheless offer but little resistance to subterranean passage. The greatest diameter in most fossorial forms lies near the shoulder, due in part no doubt to the necessary strengthening of the shoulder girdle. This is true of the mole; in other forms, such as the echidna and platypus (Fig. 49), the breadth of the stout body brings the greatest diameter further back, but in

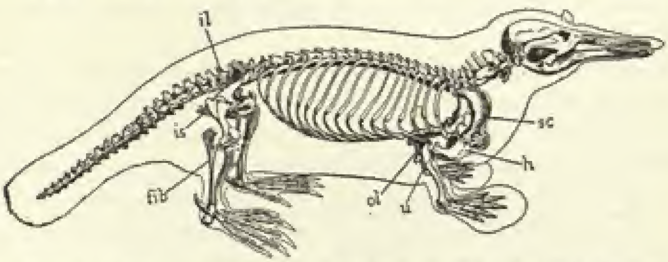

FIG. 49.—Skeleton of platypus, *Ornithorhynchus; fib*, fibula; *h*, humerus; *il*, ilium; *is*, ischium; *ol*, olecranon; *sc*, scapula; *u*, ulna. (After Pander and D'Alton.)

neither of the latter instances is the fossorial adaptation so extreme as in the former. Legless forms, snakes, lizards, and cæcilians, have a cylindrical body.

Forward of the shoulder the head tapers rapidly so that the contained skull is subconical and lacks the widely expanded zygomatic or cheek arches of many surface types. This last feature, however, is correlated also with the feeble jaw musculature, as almost all wholly fossorial types subsist upon feeble prey such as insects and worms, which require little strength of jaw or tooth.

Tail.—The tail, even in semi-fossorial animals, is usually short, for not only would a long tail seriously incommode a subterranean

creature, but its chief uses in the mammal seems to be in connection with a cursorial habit, hence there is manifestly little need of its development in forms in which no premium whatever is placed upon speed. Thus in the hedgehog, ratel, and woodchuck the tail is short, while in the wombat and the several moles it is vestigial. The tail of subterranean forms may have its uses, for it is said to serve as a valuable tactile organ.

Eyes and Ears.—In truly fossorial types the eyes, through disuse, tend to become vestigial. They would also be a source of injury in burrowing forms were they well developed. Two factors determine in general the degree of visual reduction, the duration and completeness of subterranean life. Thus "in the pocket-gophers (Geomyidæ) and Bathyergidæ the eyes are small; in [the mole-rat] *Spalax typhlus* they are mere black specks among the muscles (although retaining a relatively complete structure); in the marsupial mole (*Notoryctes typhlops*) they are imperfectly developed and functionless; in *Talpa* they are vestigial; in the Cape golden mole (*Chrysochloris*) the eyes are covered with skin" (Shimer).

The external ears also tend to disappear as in aquatic types, for not only is their position such that they would be a decided obstruction to burrowing, but they would tend to gather the soil within the ear and thus obstruct rather than aid in the collecting of sound waves, and further, their true function, just mentioned, can only be effectively rendered in the open air. Hence in the Geomyidæ and the otter, which is also aquatic, the external ears are small, in the ratel (*Mellivora*) they are very minute, in the Bathyergidæ (Cape mole-rat, etc.) they are reduced to a slight fringe of skin around the aural aperture, while in the wholly fossorial moles all three sorts are bereft of external ears entirely, which is equally true of the Monotremata. The last-mentioned group, however, are so very primitive that they may never have had them.

Digging Mechanism.—The *snout* forms an important organ for digging in the swine and in the hog-nosed snake (*Heterodon*), in each of which the organ is truncated and upturned at the tip. In the swine and in the mole *Talpa* there is a prenasal bone developed at the tip of the cartilage of the nose. This bone doubtless serves the same purpose in each instance, that of reinforcing the snout as an aid in digging.

The *incisor teeth* particularly, and sometimes the canines (swine), form very adequate fossorial organs. If the incisors, they are usually procumbent or forwardly directed as in the pocket-gophers and thus protrude in such a way as to add to their effectiveness. The tusks of the elephants, as has been mentioned, and the procumbent lower tusks of the shovel-tusked mastodons in particular, were very effective digging instruments if one may judge from the manifest wear to which they have been subjected.

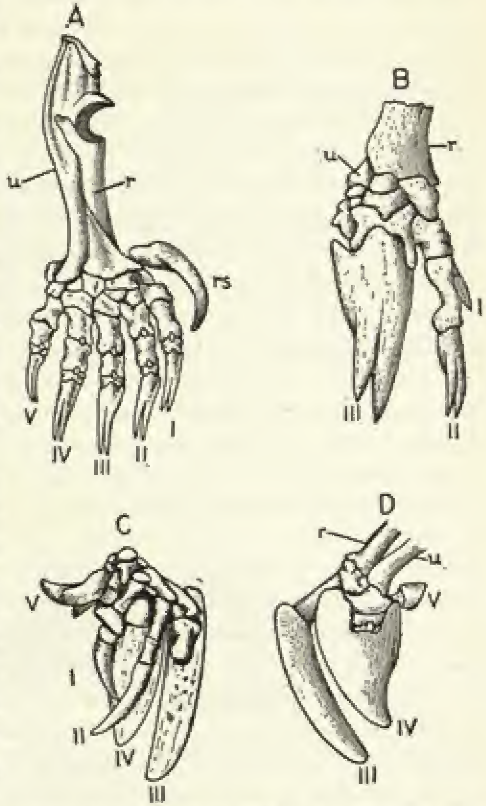

Fig. 50.—Hands of moles. A, common mole, *Talpa europæa*, after Beddard; B, golden mole, *Chrysochloris*, after Pander and D'Alton, from Abel; C, palmar aspect, and D, dorsal aspect of marsupial mole, *Notoryctes*, after Carlsson, from Abel. I–V, digits; *r*, radius; *rs*, radial sesamoid (os falciforme); *u*, ulna.

The *fore limbs* are by far the most important fossorial organs of all, hence their development and modifications have reached an extreme. All of the limbs are very short and stout in wholly fossorial forms, for not only is the speed which length of limb implies unnecessary, but long limbs would be a positive detriment in a form working in such close quarters as the average burrow. Length would also increase the mechanical disadvantage which always accompanies a lever whose weight arm is long in proportion to the power arm. In some semi-fossorial types, on the other hand, such as the hares and the pig-footed bandicoot, there is need of speed sufficient to offset

the advantages afforded by short limbs in their partial subterranean life.

The hand particularly is broad and stout, with long claws, and it differs materially from the foot, as the two members have undergone divergent specialization, the hand loosening the earth while the foot not only throws it further backward but also serves to drive the creature ahead and resists the occasional backward thrust received from the hands. In the common mole, *Condylura*, the hand is as broad as the entire body is high, so that a single sweep of this very efficient organ will clear a space wide enough for entrance, hence the digging is very rapidly accomplished. This broadening of the hand in the mole and in the echidna is effected not only by having all of the original five fingers fully developed, but by the further addition of a bone (*os falciforme*) which increases the breadth of the palm materially (see Fig. 50). In the golden mole (*Chrysochloris*, Fig. 50,B) there are but four fingers, of which the two middle ones are greatly enlarged and bear powerful claws, so that while the hand is not broadened it is still very effective.

The bones of the fore limb are always very strong, with prominent tuberosities for muscular attachment. This is especially true

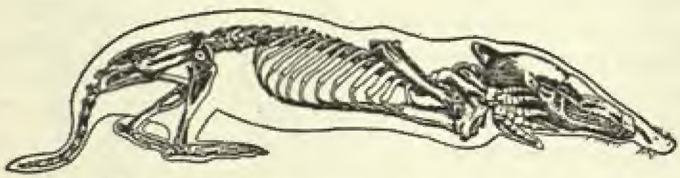

FIG. 51.—Skeleton of common mole, *Talpa europaa*. (After Pander and D'Alton.)

of the ridges at the proximal end of the humerus, which serve for the insertion of the powerful shoulder muscle, and those which aid in rotating the hand. The olecranon process, which is the extension of the ulna beyond the elbow-joint, is notably large in fossorial forms, as it is the insertion of the powerful triceps muscle which serves to straighten the arm, hence the greater the olecranon the more effective the leverage (see Fig. 51). One peculiarity of wholly fossorial forms lies in the narrow shoulders, for the fore limbs must not dig too broad a burrow and yet must be sufficiently developed to have adequate leverage. As a consequence the shoulder sockets must be as near each other as possible, and this is effected in one

of two ways: generally by a shifting forward of the entire shoulder girdle and upon the neck, as in the monotremes and northern moles (Figs. 49 and 51); or, as in the golden mole (*Chrysochloris*, Fig. 50,B), by a hollowing out of the walls of the chest, the ribs and sternum (breast-bone) being convex inward instead of outward. The shifting forward of the shoulder in the true mole is accomplished through the elongation of the first sternal segment (*manubrium sterni*), carrying with it the remarkably short clavicles or collar-bones. A powerful shoulder is essential to resist the great muscular strain, hence in digging types, as in those which climb and fly, the clavicles are retained and are fully developed. In the monotremes, not only are the clavicles present, but they are reinforced by a large T-shaped episternum and a pair of powerful coracoids which extend from the shoulder socket to the presternum (see Fig. 49). In no other mammals do these latter reptilian elements reach the breast-bone, but they are generally represented by vestigial processes. Emphasis has been laid upon the retention of many primitive features by the monotremes and much of this may be due, as in the present instance, to their fossorial mode of life. It is sometimes difficult, however, clearly to distinguish cause and effect.

The divergence of function which has been emphasized between fore and hind limb has resulted in a decided difference in their relative power. In the *hind limb* the femur is by no means as robust as the humerus, nor are its tuberosities for muscular attachment so excessively developed as in the latter bone. Greater strength is given to the lower leg by a partial fusion of the tibia and fibula, and the calcaneum or heel bone is very prominent, as the increased leverage thus gained aids very largely in pushing the animal forward by extending the foot more powerfully. In the mole *Talpa* there is a large sesamoid bone at the side of the tibia corresponding to the *os falciforme* of the hand, but otherwise the foot exhibits none of the great modification which the hand has undergone. In the hind limb of the monotremes there is an unusual extension of the proximal end of the fibula beyond the articulation at the knee, comparable to the olecranon process at the elbow and doubtless subserving the same mechanical need (see Fig. 49).

As the stress is largely transmitted from the hind limbs forward in the direction of the axis of the body in subterranean creatures, instead of vertically in opposition to gravity as in most terrestrial

forms, the *ilium* and *ischium* have become elongated in the fore-and-aft direction and lie parallel to the vertebral column instead of forming an angle therewith as usual. The ilium is also fused, usually throughout its entire length, with the sacrum, which in some forms, notably the armadillos, consists of a large number of coössified vertebræ.

In addition to the firm fusion of the sacral *vertebræ,* those of the loin and neck also tend to coössify to give greater strength and firmness in pushing the animal through the earth. It is also possible that the peculiar intercentral ossicles between the lower portions of the lumbar vertebræ of the mole *Talpa* and the hedgehogs (Erinaceidæ) may be of use in strengthening the vertebral column. Such structures are comparatively common among reptiles, but are extremely rare among mammals except in the tail. The neck vertebræ vary, for in the wombat (*Phascolomys*) and the armadillos the cervicals are wide and depressed, and in the latter several of them are commonly fused together or anchylosed as in the whales. In the mole the fourth, fifth, and sixth cervicals are much elongated and overlap each other. This region of the neck is that covered by the forward-shifted shoulder girdle, which undoubtedly accounts for this modification. The transverse processes of the lumbar vertebræ and the muscles which are attached to them exhibit comparatively little development, as the strains transmitted are largely longitudinal with little or no lateral movement.

Hibernation.—Winter sleep is a necessity on the part of subterranean animals living beyond the limits of the tropics, because of the absence of green vegetation which forms either directly, or indirectly by supporting insects and worms, the mainstay of their diet. Digging through frozen soil would be so insuperable a task that it is also prohibitive of active underground life. An exception to this rule would be the lemming (*Myodes lemmus*) whose "food is entirely vegetable, especially grass-roots and stalks, shoots of the dwarf birch, reindeer-lichens, and mosses, in search of which they form, in winter, long galleries through the turf or under the snow" (Flower and Lydekker).

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CHAPTER XX

AQUATIC ADAPTATION

Primarily Aquatic Vertebrates

By primarily aquatic forms is meant the fishes, which have never had a terrestrial ancestry, but have evolved from more primitive aquatic progenitors. As a consequence their adaptation to a watery medium is perfect and they do not suffer as those secondarily adapted do through their inability to breathe water. They are, therefore, the primitive gill-breathing vertebrates, sometimes with accessory air-breathing organs, it is true, but retaining the gills as the chief or only respiratory organs throughout life. But this is not all, for the dense medium in which they live has exerted so profound an influence upon them that, with some exceptions which only serve to emphasize the rule, they are stamped in a common mould, giving them so great a similarity of form that no one fails to recognize a fish.

Contour in an aquatic vertebrate is all-important, for nature as a marine architect conforms to rules of mathematical precision, the study of which has aided very largely in ship designing. The head, body, and tail are compressed into a beautifully curved stream-lined form, the entire surface of which is accurately rounded, with no protuberances which would retard the swift passage of the animal through the water. The head is sub-conical, the edges of the jaws and gill-covers fit precisely, and even the eyes conform accurately to the curvature of the head. Viewed from the front, the outline of a typical swiftly swimming fish like the Spanish mackerel (*Scomberomorus maculatus*, Fig. 52) is a perfect ellipse, and the fins which are so prominent when viewed from the side can scarcely be seen, as they are reduced to thin keel-like lines. The greatest circumference of the fish is approximately 36 per cent of the length, measured from the snout, the "entering angles" being very similar for a great many different fishes. From the point of greatest cross-section the lines of the "run," as it is called, are also very similar—smooth, hollow curves which freely permit the return of the displaced water.

Locomotion is effected by lateral undulations of the flexible body, aided by the fins. The latter are not, therefore, primary but accessory locomotive organs. The body is thrown into a series of alternate curves which begin at the head, pass along the body, and disappear at the tail. The static water enclosed in the incurved places is pressed upon, causing the fish's forward movement. Of course in an ordinary fish there is some lost motion or "slip," for the water is not sufficiently resistant to oppose the thrust of the body, but in the larval eel, which is a thin ribbon-like creature whose great relative depth presents a large lateral surface, the swimming is so precise that if a pencil is held in one of the hollows the fish's body passes without touching it at all. The other extreme is seen in the swimming efforts of an ordinary snake which,

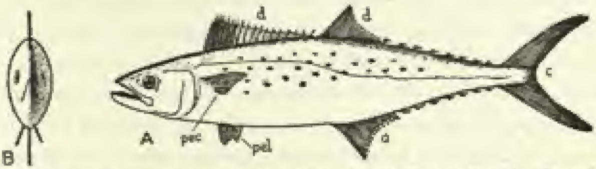

FIG. 52.—Type of swift-swimming fish, Spanish mackerel, *Scomberomorus maculatus.* A, side view: *a*, anal fin; *c*, caudal; *d*, dorsal; *pec*, pectoral; *pel*, pelvic. B, front view. (After Goode, from Dean.)

while it does progress, loses a great deal of motion because its lateral surface is not sufficiently great.

This increase of resistant surface is obtained in the fish through the development of the unpaired fin-folds of the skin, stiffened by fin-rays of elastic bone or cartilage. These unpaired fins may be more or less continuous from the head along the mid-line of the back, around the tail and forward along the under side as far as the vent. Usually, as in the Spanish mackerel, this continuous fin-fold is broken up into a number of distinct fins, developed where stresses arise, and disappearing where there are none. The fins along the back are known as dorsal, that around the tail as caudal, and that beneath the body as anal. Of these the caudal is by far the most important as a propelling organ. The mackerel also shows horizontal keel-like ridges on either side of the tail.

The fish also has lateral or paired fins corresponding to the fore and hind limbs of the terrestrial vertebrate. Of these the pectoral fins lie just behind the gill apertures at the shoulder, while the

pelvics are more variable in position, though normally they should lie on either side of the vent. The paired fins when held out from the body may be simple keels like the unpaired fins; the pectorals especially, however, may have additional functions, as they serve as stabilizers and also to check the animal's way. Perhaps the primitive function of the paired fins was to maintain a horizontal position, as the removal of the pectorals tends to make the fish dive, and of the pelvics, to rise to the surface.

Swim-Bladder.—As a further adaptation to aquatic life all fishes above the sharks may have a structure known as the swim-bladder —a hollow organ filled with air or gas, the present function of which is largely hydrostatic, in that it maintains the fish at a certain depth of flotation. If the creature wishes to sink, the body is slightly compressed through muscular contraction, and with it the swim-bladder. This lessens the bulk, and the weight remaining constant, the specific gravity is increased, with a resultant loss of buoyancy. Relaxation of the muscles has the contrary effect, the compressed gas in the bladder expands, increasing the fish's size and thereby decreasing the specific gravity, and the creature rises. The principle is comparable to the method whereby the depth of flotation of a submarine vessel is controlled, although the mechanism differs, for here water is admitted to the ballast tanks to be driven out again by compressed air, and thus the ship sinks or rises as the case may be.

The swim-bladder is an outgrowth of the alimentary canal and is a very important organ in the evolution of higher forms, for it is the homologue of the lung of the terrestrial animal, and there can be no doubt that the air-bladder of certain ancient fishes, the primal function of which may well have been respiratory rather than hydrostatic, actually evolved into a lung when the drying up of the waters left them stranded and they were forced to become air-breathing. Thus arose the progenitors of all terrestrial vertebrates (see Chapter XXIX).

Secondary Aquatic Adaptation

Secondarily aquatic forms are the lung-breathers which, through stress of circumstances—inhospitable lands where food was scarce or competition severe—were forced to return once more to the primal home of their remote ancestors. There is always, as has been said, the handicap of lung-breathing, but otherwise the adap-

tation of certain of the more extreme forms is little short of marvellous.

As an offset to this handicap it should be remembered that lung-breathing made possible or at least accompanied a tremendous advance in other organs and their functions, such as a higher brain with a consequent psychological advancement. When the lung-breathers turned back to the waters, they readopted only the externals of fish life, but kept in varying degrees the higher brain and the more efficient methods of aëration of the blood and of locomotion. And again and again they easily won a place on the lower level against the most highly specialized of the inferior grades.

Amphibious vertebrates, as the name implies (Gr. ἀμφί, double, and *βίος*, life), spend part of their time on land and part in the water. They are really terrestrial forms, showing partial aquatic adaptation only, which rarely extends beyond the possession of webbed feet and a laterally compressed swimming-tail, which may bear a fin-like expansion along its upper margin, and sometimes a lack of ossification of certain of the wrist and ankle bones. The class Amphibia, which embraces the historically transitional forms in the original landward migration, modified representatives of which still exist, breathe typically by means of gills during their youth, and sometimes throughout their life. Others abandon their gill-breathing at the approach of maturity and become as essentially terrestrial as a reptile.

Instances of amphibious life among forms above the class Amphibia are numerous, but one or two instances will suffice. The Galapagos lizards (Fig. 53) which were mentioned in Chapter IV are instances of forms terrestrial from choice but aquatic from necessity, for, it will be remembered, they live on certain rocky islands of the Galapagos group, swimming out to the surf line and diving for the sea-weed upon which they feed. There is evidently no menace to their safety ashore but their aquatic excursions seem to be made in actual dread of bodily injury, as their behavior indicates. Here a flattened swimming-tail and slightly compressed body are the extent of their aquatic adaptation.

Another instance wherein the habits are inferred rather than the result of observation is that of the late Cretaceous hadrosaurs (see Chapter XXXI), a group of dinosaurs of which our knowledge is very complete, for not only have all parts of the skeleton and

dentition been preserved to us, but fossilized mummies as well (see Chapter XXV), creatures which died in the open and simply dried up so that bone and sinew, hide and even portions of the flesh have been preserved in great detail. These creatures had a wonderful battery of teeth, an adaptation to a very harsh herbage, presumably the Equisetales or horsetail rushes which are found preserved with them. There is evidence of adaptation to submerged, underwater feeding on the part of the hadrosaurian dinosaurs, which, together with the splendid swimming-tail, webbed

FIG. 53.—Galapagos sea-lizard, *Amblyrhynchus cristatus*. (After Brehm, from Williston's *Water Reptiles*.)

hands and feet, imply an aquatic or at least amphibious type. Add to this the fact that the creature was defenseless, utterly devoid either of weapons or armor, and that its arch-enemy *Tyrannosaurus* was also terrestrial, and we have evidence which points to a reversal of the life conditions of the Galapagos lizards, for with the dinosaur food was on land, and safety and retreat in the waters. One would therefore expect the greater relative degree of aquatic adaptation which they show.

The marine turtles (Fig. 54) have gone a long step further in that here both food and safety are found at sea and only one need, which does not concern all, but only the females, that of

egg-laying, brings them to the land at all, and this annual shoreward migration is fraught with dire peril which nothing but the most urgent summons would cause them to face. There is reason to believe, moreover, that in some species the males never come ashore.

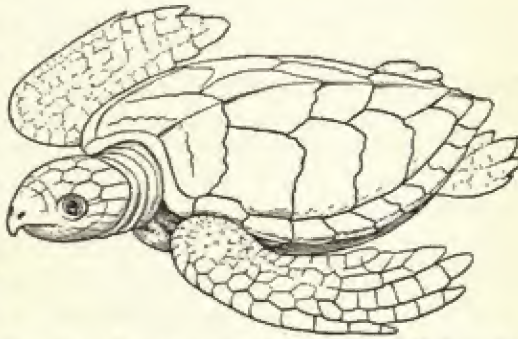

Fig. 54.—Marine turtle, "hawksbill," *Chelone imbricata*. (After Haeckel.)

The final stage in reptilian adaptation was shown by the ichthyosaurs (Fig. 55) of the Mesozoic whose perfection for their life conditions equalled that of the modern whales, even to the utter abandonment of shore going, for there is abundant evidence from the contained embryos in several known specimens that these medieval high-seas corsairs brought forth their young alive and therefore did not need to go ashore for egg-laying. This is a necessary part of ultimate aquatic adaptation, for no egg laid by a truly air-breathing vertebrate (*i. e.* allantoic egg, see page 456), can be hatched in the water, as the enclosed embryo would drown as certainly as would a submerged adult.

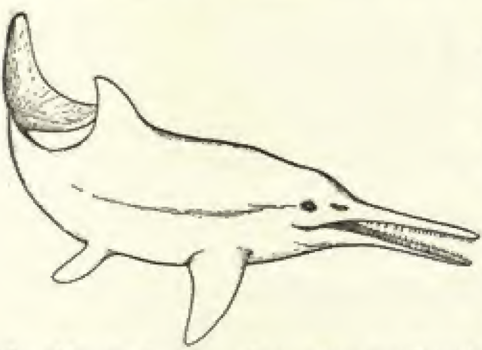

Fig. 55.—Ichthyosaur. Restoration by Knight. (From Schuchert's *Historical Geology*.)

A list of secondarily aquatic vertebrates follows:

Class Reptilia

	Amphibious	*Aquatic*
Order Chelonia	Swamp and river turtles	Sea-turtles
Order Sauropterygia	Nothosaurs	Plesiosaurs
Order Proganosauria		All

Class Reptilia—Continued

	Amphibious	Aquatic
Order Ichthyosauria		All
Order Thalattosauria		All
Order Parasuchia	Phytosaurs	
Order Crocodilia	Crocodiles and alligators	Extinct sea-crocodiles
Order Squamata	Marine iguanas Mosasaurs	
Order Dinosauria	Amphibious sauropods, hadrosaurs	
Eight orders		

Class Aves

Order Odontolcæ		*Hesperornis*
Order Ichthyornithes	*Ichthyornis*	
Order Pygopodes	Loons and grebes	
Order Impennes		Penguins
Order Tubinares	Petrels, albatross, puffins, etc.	
Order Steganopodes	Gannet, cormorant, frigate bird, pelican	
Order Herodiones	Flamingo	
Order Anseres	Ducks and geese	
Order Gaviæ	Gulls, terns, auks	Great auk
Nine orders		

Class Mammalia

Order Monotremata	*Ornithorhynchus*	
Order Marsupialia	Water opossum (*Chironectes*)	
Order Insectivora	Aquatic shrews, desman, etc.	
Order Rodentia	Muskrat, water rat, beaver, capybara, etc.	
Order Carnivora		
Suborder Fissipedia	Sea otter, otter, mink, etc.	
Suborder Pinnipedia		All
Order Cetacea		All
Order Ungulata	Hippopotamus	
Order Sirenia		All
Eight orders		

Thus there are twenty-seven orders of secondarily adapted water-inhabiting vertebrates all told, some of which are exclusively aquatic. Many of these, of course, are now extinct, so that the whole number is far in excess of those of any one time. Of aquatic lung-breathers, the honor falls to the reptilian order Proganosauria, which are the first in point of time, as their remains are found en-

tombed in rocks of Permian age not very long, relatively, after the reptiles were established.

Body Contour.—As in primarily adapted forms, the body contour becomes stream-lined, the neck constriction disappears, the tail enlarges, and the same "numerical lines" prevail. This assumption of the fish-like form is best seen in the fully aquatic orders—Ichthyosauria, Cetacea, Sirenia, Pinnipedia—and to a lesser extent in several other groups. The minor factors contributing to this general effect are, first, *skull modification*. This includes a shortening of the cranium or brain-case, which becomes proportionately higher and wider, with a consequent effect upon the proportions of the brain, which is likewise short and wide. The facial portion of the skull, on the contrary, tends to elongate so that many forms, especially those which subsist upon active prey, as the porpoises and ichthyosaurs did, have an elongated slender snout or rostrum. The zygomatic or temporal arch in the Cetacea is also reduced almost to a vestige.

The *neck* shortens very materially and there is a loss of mobility in the swifter, tail-driven types. In those forms like the plesiosaurs, whose paddle propulsion was necessarily slower, an elongated, supple, darting neck was necessary to overtake the swiftly moving prey. In the whales, while the number of cervical vertebræ is the standard mammalian seven, they may be fused into a solid, compressed mass of bone, whereas the neck of the manatee among Sirenia, with but six cervicals, forms one of the three exceptions to the standard number, the other two, as we have seen, belonging to the sloths.

In old-fashioned reptiles derived from primitive stocks which early became adapted to aquatic life, such as the ichthyosaurs, the *vertebræ* retain their ancient simplicity, having simple biconcave bodies or centra like those of fishes. In higher forms the vertebræ tend to simplify secondarily, due to the fact that the body, being water-borne, is equally supported throughout, hence the vertical stresses which are the result of gravity in land animals are practically eliminated, and the thrust or driving force is transmitted longitudinally through the column. This simplification includes the centra or bodies of the vertebræ and especially the secondary articulations or zygapophyses. The several processes may become reduced in the trunk region but elongated in the tail to provide greater area for muscular attachment.

The *sacrum*, that portion of the vertebral column which articulates with the pelvis and which, therefore, in land animals has to withstand and transmit the supporting impact of the hind limbs, is more or less reduced in direct ratio to the loss of supporting or propelling function on the part of these appendages. Thus, in the ichthyosaurs, cetaceans, and sirenians the sacrum cannot be distinguished from the other vertebræ and while its approximate locality cannot be far from the vent, the actual identity of the former sacral vertebræ is lost.

The *chest* of the truly aquatic type tends to become cylindrical; land forms, on the other hand, generally show lateral compression, especially if they are quadrupedal in their mode of progression, with the body off the ground. The chest in aquatic types is also modified in such a way as to bring the internal cavity higher to-

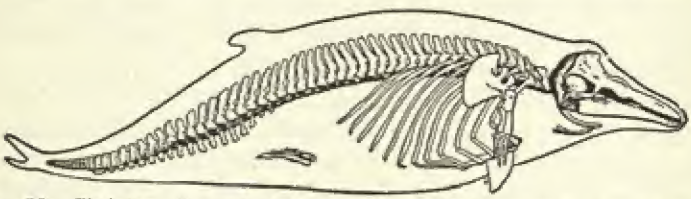

FIG. 56.—Skeleton of porpoise. The vestigial pelvic bones are shown embedded in the flesh. (After Pander and D'Alton.)

ward the back. This insures greater stability of flotation and increased lung capacity and is accomplished by the ribs tending to become highly arched dorsally and then to move upward from their point of attachment on the centra to the transverse processes. A gradation in this last feature may be demonstrated by taking first the ichthyosaurs, wherein the rib articulation is entirely central, both rib facets—that for the capitulum or head and that for the tuberculum—being on the body of the vertebra, a unique feature which makes an ichthyosaur centrum unmistakable. In the Pinnipedia the position is transitional, whereas in the whalebone whales the articulation of ribs and vertebræ is extremely loose, probably to allow great mobility of the chest for the rapid respiration necessary after prolonged submergence. In the Sirenia and Cetacea the diaphragm has become horizontal in position instead of being practically vertical as in most quadrupedal mammals.

The *bones* of swimming forms tend to become light and spongy, the interstices in those of the whales being filled with oil. Excep-

tions to this are found in forms which, like the walrus and Sirenia, derive their sustenance from the bottom, the walrus feeding on molluscs, the sea-cows subsisting on submarine vegetation just as their bovine namesakes graze in terrestrial meadows. This necessitates a ballasting which is secured by increased weight of bones, like the great, wide, massive ribs of the manatee.

Externally, the secondarily adapted sea-vertebrate is characterized, like the fish, by the elimination of retarding excrescences, hence in the course of their evolution aquatic mammals have lost all trace of *external ears*. This not only renders the contour of the head smoother, but removes a practically useless appendage, for the pinna of the ear has for its especial use the collection of aërial sound waves, a function which is valueless in a submerged form. Thus the ears are reduced in amphibious mammals, and are totally lost in the whales and true seals and walrus, though retained in reduced condition in the sea-lions (Otariidæ) which spend much of their time ashore. The occasional atavistic occurrence of external ears in the porpoise has been noted.

The *external nostrils* or nares tend to forsake their old terminal position at the end of the snout and move toward the apex of the head as in most of the whales, ichthyosaurs, phytosaurs, and mosasaurs, mainly in forms with reduced mobility of neck in which the vertex of the head first appears above the surface of the water. This one feature is invariably indicative of aquatic life. The nostrils are often capable of being closed, as is also seen in desert-adapted forms like the camel as a protection against drifting sand.

The *eyes* in amphibious types also tend to shift higher on the face as in the hippopotamus, whose nostrils, eyes, and ears can appear above the surface of the water while all the rest of the head and body remains submerged. The advantage of this is obvious. In truly aquatic types, on the other hand, the eye does not shift its position, as aërial vision has largely lost its importance, but instead of this the eyes become adapted to aquatic vision which, because of the denser medium, requires a different curvature of the lenses. They adapt their vision to the air by contracting the pupil to a narrow slit, vertical in the seals and horizontal in the whales, or by an actual shifting of the position of the crystalline lens. Penguins which pursue their prey submerged are curiously limited in their aërial vision.

Locomotive Mechanism.—Fleshy, fin-like expansions of the body-wall occur in the whales and ichthyosaurs and also probably in the extinct thalattosaurs and sea-crocodiles (thalattosuchians) (see Fig. 60, *Geosaurus*). These *fins*, as in fishes, may be dorsal

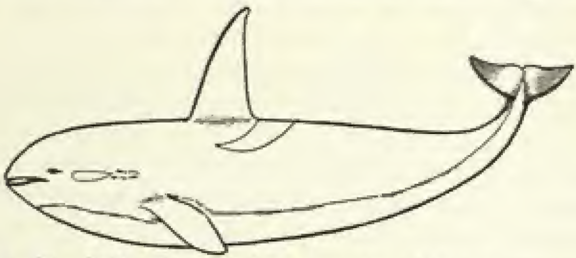

FIG. 57.—Killer whale, *Orcinus rectipinna*. (After Scammon.)

and caudal. The dorsal fin is a triangular structure, essentially equilateral in the ichthyosaur, very high and narrow in the killer whales, especially *Orcinus rectipinna* (Fig. 57). On the other hand, some whales such as *Delphinapterus*, the white whale, and *Balæna*, the right whale, lack the dorsal fin entirely; while in the sulphur-bottom, *Balaenoptera musculus*, the fin is small and situated well aft upon the tail. The development of this fin must be entirely a response to mechanical needs and correlated with a certain bodily form and peculiarity of locomotion, just as the deep fin-keel of a sailing yacht would be superfluous upon a motor-driven craft.

Secondarily aquatic types very often go back to first principles and readopt the old wriggling or undulatory motion of their pristine ancestors, to which fins, etc., are only subsidiary. This also accompanies elongation of body, multiplication of segments, and loss of limbs (as in the zeuglodonts and many long-tailed aquatic types).

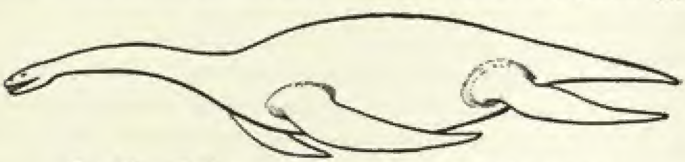

FIG. 58.—Plesiosaur, *Cryptocleidus*, restored by Knight.

Thus two methods of propulsion are seen among aquatic types, even in those whose adaptation has passed the amphibious stage. Williston has called them "oar propulsion" and "tail propulsion." In the former, exemplified by the turtles and plesiosaurs (Fig. 58),

the limbs are more nearly equivalent in size and propulsive power than in tail-propelled types. In the latter, which is included in the undulatory form of locomotion, that seen in the ichthyosaurs, whales, and sirenians, the hind limbs tend to disappear until finally no external vestige is discernible, though slender bones, representing the pelvis, thigh, and sometimes the tibia, may be found deep buried within the flesh (see Figs. 56 and 182).

It is characteristic of secondarily aquatic vertebrates that where unpaired fins are developed they are never supported by the skeletal elements, known as fin rays, as they are in fishes; they may, however, be strengthened by masses of dense connective tissue.

The ichthyosaurs were extinct forms ranging in time from the Triassic to the late Cretaceous. The earlier species moved largely by means of the limbs, the later ones almost exclusively by the tail. In the former the hind limbs were nearly as large as the front ones, while in the later ichthyosaurs, as the tail developed the hinder paddles were reduced in size until they were often very much smaller than those in front. More than eighty years ago Sir Richard Owen, the great English anatomist, noticing a curious downward dislocation of the tail at its mid-length in many articulated skeletons, came to the conclusion that the ichthyosaurian tail must have borne a terminal fleshy fin quite like that of the whales and sirenians, but it was not until forty years later that specimens showing the actual outline of the body and fins were found and Owen's conjecture verified. His only error lay in the supposition that the caudal fin was horizontal like those of the mammals, whereas it is vertical like that of a shark. The ichthyosaur tail is diametrically opposed to that of the shark, however, for in the latter the backbone is deflected upward into the superior lobe of the fin, whereas in the former it extends along the front margin of the lower one. This may be due to the fact that the caudal arose as a low fin-like expansion along the upper side of the tail, not an uncommon thing among air-breathing vertebrates, and ultimately developed into the widely expanded fish-like fin of the later forms. The diagram of the ichthyosaur caudals will make this clear (see Fig. 59).

The Thalattosuchia or sea-crocodiles were a short-lived race, their remains being confined to the rocks of Upper Jurassic age in Europe. They were also of moderate size compared with other

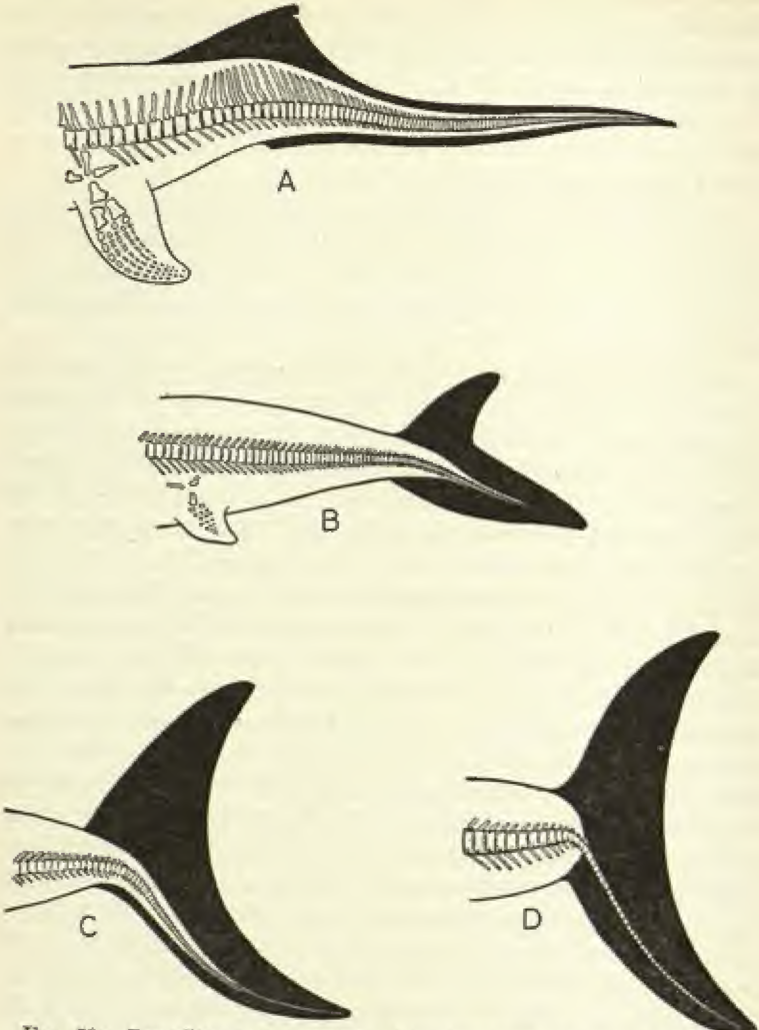

FIG. 59.—Propelling tails, caudals, of ichthyosaurs, showing the development of the organ. A, *Mixosaurus nordenskjöldi*, Trias, Spitzbergen; B, *Ichthyosaurus quadriscissus*, young, Upper Lias, Württemberg; C, same species, adult; D, *I. trigonus* var. *posthumus*, Upper Jurassic, Solenhofen, Bavaria. (From Abel.)

marine vertebrates, ranging from 10 to 20 feet in length. But few forms are known, of which *Geosaurus* (Fig. 60) is perhaps the most typical. This type shows a sharp downward bend toward the end of the tail as in the ichthyosaurs and the inference that like them the creature bore a well developed caudal fin is undoubtedly correct. Strangely enough, however, the hind limbs were much larger than those in front, probably a character inherited from its shore-dwelling ancestry.

The caudal fin of the marine mammals differs markedly from that of the reptiles in being horizontal instead of vertical and in the symmetry of its two halves or flukes, the bone dividing the tail into two equal parts rather than running into one lobe to the exclusion of the other. In the Sirenia the same is true, the manatee

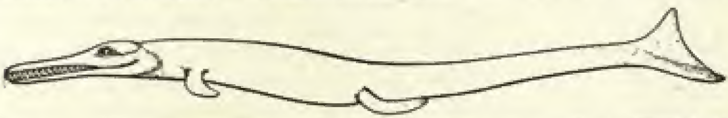

FIG. 60.—Marine crocodile, thalattosuchian, *Geosaurus*. (From Williston's *Water Reptiles*.)

having a rounded tail, while in the dugong (*Halicore*) and the exterminated Steller's sea-cow (*Rhytina*) it was notched like that of a whale.

Limbs.—Webbed feet are the first natatorial adaptation, and the degree of webbing is a very variable thing. It may consist simply of lobe-like lateral expansions of skin on either side of the toes, as in the coot, or of actual connections from digit to digit. Extreme aquatic adaptation, on the other hand, implies the development of a paddle in which there is a loss of mobility of the various joints, the entire skeleton of the limb being enclosed by the skin in a single mass showing no external divisions into fingers and toes. The result is the production of a flexible paddle of great aquatic utility, but ill adapted for coming ashore. As a further modification the individual phalangeal bones increase in number (hyperphalangy) and, in some instances, one or more additional rows are seen, as though extra toes over the normal five had been added (hyperdactyly). There is also a change in relative proportions of the various segments as in cursorial adaptation, the humerus or femur diminishing in length while the other individual bones may shorten much more, although from their increase in numbers the area represented by the digits may become very

much extended. In some instances, as an especial modification, for example, in the round-headed dolphin, *Globicephalus* (see Fig. 13,C), while the length of two or three of the digits may be very great, the others may be much reduced.

The reduction of the hind limbs with the development of the tail has been mentioned, together with their total loss externally in the aquatic mammals. Not only are their vestiges discernible in the form of the bones hidden in the flesh, but as Kükenthal has shown, external traces (*Anlagen*) of them are visible in fœtal whales (*Megaptera*, the humpback whale) on either side of the vent.

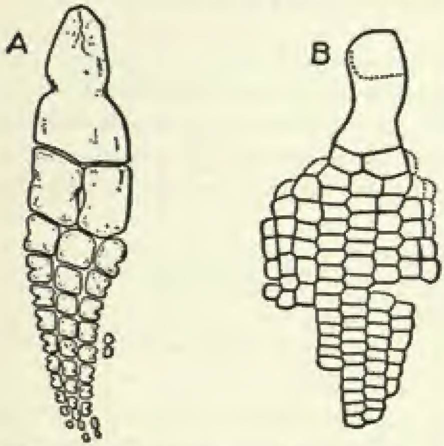

FIG. 61.—Ichthyosaur paddles. A, left anterior paddle of *Merriamia zitteli*, Trias, California. (After Merriam, from Abel.) B, same, of *Ichthyosaurus platydactylus*, Lower Cretaceous (Aptian), Germany. (After Broili, from Abel.)

Integument.—The modification undergone by the skin in aquatic animals is in the line of reduction of armoring, of hair, of skin glands, muscles, and nerves. *Loss of armor* has taken place in the ichthyosaurs, for reptiles are primitively armored and in the wonderfully preserved specimens from Holzmaden, Bavaria, the only remaining traces lie on the anterior edge or cutwater of the fins, and, in one specimen at least, along the mid-dorsal line from the head to and on either side of the dorsal fin.

The *loss of hair* is characteristic of marine mammals, and the reason seems to be that whereas hair is a wonderfully good nonconductor of heat when dry, in that it retains a blanket of still air around the body, it is of little value in the water. Hence the fur seals (Otariidæ) which retain more terrestrial characters than do the hair seals (Phocidæ), such as the external ear and the ability to use the hind limbs for progression on land, still wear a thick under coat of fur—the sealskin of commerce. The hair seals with their more perfect aquatic adaptation come ashore more rarely

and have lost the furry under coat entirely, retaining simply the so-called contour hairs, so that their hides are valueless as fur although used for other purposes. The whales and sirenians have lost all traces of hair except perhaps a few bristles around the mouth, but most of them are well covered with fœtal hair before birth, which points to an ancestrally hairy condition. In a few instances, such as the white whale or Beluga and the narwhal, even the fœtus has lost its hair, thus showing the extreme of specialization.

As a compensation for the loss of hair, the mammals have developed a *layer of fat* in the connective tissue beneath the skin (subcutaneous tissue) and this serves admirably for the retention of the bodily heat which would otherwise radiate out very rapidly into the surrounding water. Even with this device much heat apparently is lost, for one of the greatest impediments experienced in shipping to New York porpoises caught on the coast of the Carolinas was the difficulty of keeping the water in the shipping tanks, and therefore the animals contained in them, sufficiently cool for health. This shows that the porpoises develop so great an excess of heat that a more efficient heat-retaining integument is not necessary; the heat excess being correlated with the high speed which these animals can attain (see page 302).

Skin glands such as sweat or oil glands have their value impaired if their secretions are continually washed away, hence their reduction in aquatic animals; while the thickening and immobility of the skin has resulted in the atrophy of its muscles and nerves. The *salivary glands* of those forms which devour their food under water are also reduced, possibly because their secretions would be too largely diluted to have great digestive value, and partly because the mechanical function of lubrication to aid in swallowing is subserved by water taken in with the food.

Mouth Armament.—Except in the sea-cows and walrus the jaws, being no longer used for mastication, but only for the prehension of relatively feeble prey, have very largely lost their power, so that the coronoid process and other areas for muscle attachment are reduced. The teeth also suffer modification, usually in the direction of simplification, the increase of numbers, or on the other hand total loss from one jaw (sperm whale) or both (baleen whale). In the latter instance the function of the teeth is taken by the remarkable baleen or whalebone to be described later. The marine

reptiles have simple prehensile teeth fitted for the retention of slippery prey, except the sea-turtles whose teeth had disappeared long before their aquatic adaptation began.

The Cretaceous marine lizards or mosasaurs (Fig. 62) show a remarkable adaptation for the prehension of prey, for not only

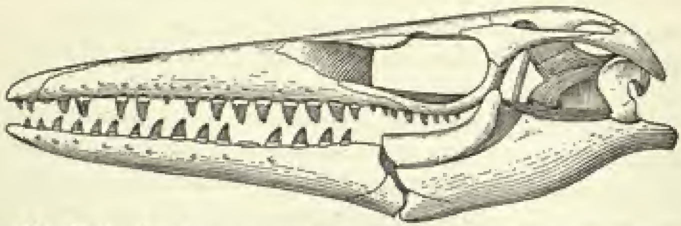

FIG. 62.—Skull of a mosasaur, *Clidastes*, Cretaceous (Niobrara), Kansas. (From Williston's *Water Reptiles*.)

were the rims of the jaws armed with slightly recurved teeth, but others were borne upon the roof of the mouth as well. The lower jaws instead of being firmly united together at the symphysis (chin) were connected by an elastic ligament and each jaw was doubly articulated with the skull through a very movable intervening bone, the quadrate. The most remarkable thing, however, was an extra joint in the mid-length of each jaw bone so that it could be bowed out into a decided curve and thus, as in snakes, effect the swallowing of prey larger than the normal gape of the mouth.

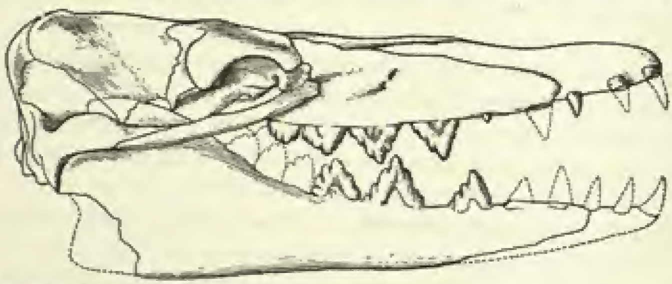

FIG. 63.—Zeuglodon skull, *Prozeuglodon atrox*, Upper Eocene (Birket-el-Qurun), Egypt. (After Andrews.)

The whales show a very interesting tooth gradation. Ancient whale-like forms (zeuglodonts) still had the tooth differentiation characteristic of mammals, the cheek or molar teeth bearing many cusps arranged in longitudinal series (see Fig. 63). In the

modern whales, in which the teeth are retained, they are generally simple cones and are as a rule much more numerous than the normal number for a placental mammal, which is forty-four, eleven in each half of each jaw. In *Globicephalus,* the ca'ing whale, the number may be over one hundred, and the dolphins, *Delphinus* and *Inia*, may have twice that number. As we have seen, the sperm whale, *Physeter*, is devoid of functional teeth in the upper jaw, in spite of the fact that it feeds upon active cephalopods (giant squid). *Monodon*, the narwhal, has but a single tooth, although its mate may be vestigial, in the form of a long, spirally twisted tusk or "horn," really a modified incisor. In the female the horn is reduced. In the curious toothed whales, *Ziphius* and *Hyperoödon*, there is but a single tooth in each mandible. The latter genus has small teeth in the upper jaw, which are also present but functionless in the former. (See Chapter XXXIV.)

In the baleen whales, which may possibly represent a distinct whale-like evolution from that of the toothed forms, the teeth are entirely absent except for vestiges in the embryo, which, however, never cut the gum. In their place there has been developed the remarkable baleen or whalebone. This is a horny outgrowth from the epithelium lining the mouth and may be compared to an exaggeration of the transverse ridges on the palate characteristic of many mammals. Each piece of whalebone is triangular, attached by its base to the roof of the mouth, with the free inner margin frayed out into numerous threads which form the straining apparatus. When the creature feeds it rushes open-mouthed through swarms of whale food or "brit" (pelagic organisms which are largely pteropod molluscs); then the mouth is partly closed and the water is forced out between the plates of whalebone by the tongue; thus the organisms are strained out and subsequently swallowed. (See Chapter XXXIV.)

The ichthyosaurs, while as a rule well toothed, also reduced the dentition so that in the American genus *Baptanodon* and the European *Ophthalmosaurus,* which were related if not identical, the teeth had become vestigial and functionless, although the germs were still present in the jaws. The convergence of the older ichthyosaurs toward the modern whales is thereby rendered all the more complete and certainly the diet of fish and cephalopods in the toothed forms, as shown by the fossil waste voided from the alimentary canal (coprolites) in the ichthyosaurs, was the same in

both instances. But the food of the toothless ichthyosaurs is harder to conjecture; there is certainly no evidence of the development of anything comparable to baleen, as has been suggested.

Precocity.—Mental precocity is as necessary in the gregarious aquatic animals as among the cursorial, and they soon show ability to keep up with the mother. The new-born young of whales are from one-quarter to one-sixth the length of the parent and a porpoise about half the length of its mother has been seen maintaining its position as readily as she at the bow of a 15-knot ship.

Speed.—Records of speed are difficult to obtain, but porpoises are known to keep pace with a 39-knot destroyer, sheering off ahead of the craft with the utmost ease, and this speed is main-

FIG. 64.—Sulphur-bottom whale, *Balænoptera musculus*, with the African elephant "Jumbo," *Loxodonta africana*, drawn to scale.

tained with, as a rule, an almost inappreciable vibration of the highly efficient propelling tail, as seen from above. (See also page 315.)

Size.—Water-borne animals exceed all others in size, for the energy exhausted by terrestrial creatures in overcoming gravity may here be turned into growth force. The largest recorded terrestrial animals which live are the elephants, of which "Jumbo," an African specimen, had a height of $11\frac{1}{2}$ feet and a weight of six and one-half tons. African elephants grow to 13 feet and the great imperial elephant of the American Pleistocene may have exceeded this by a foot. In comparison with a sulphur-bottom whale, however, with a length of 87 feet and an equivalent weight in tons, the elephant becomes insignificant (see Fig. 64). The largest strictly terrestrial dinosaur, *Tyrannosaurus*, reached a length of 47 feet and a standing height of 18 to 20 feet. The bulk of body, tail, and hind limbs was also great, but the amphibious dinosaurs exceeded it, although the disparity of size was not comparable with that of

whale and elephant. *Brontosaurus,* one of the most ponderous dinosaurs, had a length of 67 feet and an estimated weight when alive of 38 tons. *Diplodocus,* while more slenderly proportioned, was at least 87 feet long; and the remains of *Gigantosaurus* from East Africa (Tendaguru) indicate an animal nearly equalling *Diplodocus* in length and heavier than *Brontosaurus.*

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CHAPTER XXI

SCANSORIAL ADAPTATION

Need of Scansorial Adaptation.—Climbing on the part of arboreal animals is not necessarily a manifestation of ambition, but quite the reverse, in that relatively feeble creatures may take to the trees for safety and retreat and for abundant and easily procured food. Historically, arboreal life is of more than passing interest, for it is probable that practically all flying vertebrates, except fishes, were derived from scansorial types and that, on the part of the mammals at least, during the long Age of Reptiles arboreal life was the one factor more than any other that safeguarded the race and rendered its subsequent evolution possible.

The list of climbing animals is very great, but of those which show very marked adaptation to arboreal life the numbers are relatively few. A partial list is as follows:

Class Pisces

Climbing perch (*Anabas scandens*).
Mud skipper (*Periophthalmus barbarus*).

Class Amphibia

Stegocephalians from the Coal Measures tree trunks.
Tree frogs. Very large group with convergences. Cosmopolitan except for Africa.

Class Reptilia

Lizards, especially geckoes and chameleon.
Tree snakes.
"Proavian"?

Class Aves

Passerine birds.
Hoatzin.
Parrots, woodpeckers, wood-hewers, and several instances among the typically terrestrial orders.
Galliformes; cruassows, guans, chachalacas.
Gruiformes: trumpeters.
Anseriformes: tree-ducks, muscovy ducks.
Pelecaniformes: snake birds, cormorants.

Class Mammalia

Order Marsupialia.
- Didelphyidæ, opossums; all but *Chironectes*, the water opossum.
- Phalangeridæ, phalangers.
- Macropodidæ: *Dendrolagus*, the tree-kangaroo.
- Dasyuridæ: *Dasyurus*, *Phascologale*.

Order Edentata.
- Bradypodidæ, tree-sloths.
- Myrmecophagidæ, anteaters: *Tamandua*, *Cycloturus*.

Cohort Ungulata.
- Hyracoidea: *Dendrohyrax*, the tree-hyrax.
- *Agriochærus*, an extinct oreodont.

Order Carnivora
- Felidæ, cats: many partially, jaguar only, wholly.
- Viverridæ, civets, etc.: *Cryptoprocta*, *Viverra*, *Arctictis*.
- Procyonidæ: *Procyon*, the racoon; *Cercoleptes*, the kinkajou; *Nasua*, the coati; *Bassariscus*, *Bassaricyon*.
- Mustelidæ: the martens, and *Helictis*.
- Ursidæ: the brown bears.

Order Rodentia.
- Anomaluridæ, flying squirrels.
- Sciuridæ, squirrels.
- Lophiomyidæ.
- Myoxidæ, dormice.
- Cercolabidæ: only the American tree-porcupines (*Erethizon*).

Order Insectivora.
- Tupaiidæ, pen-tailed shrews.
- Erinaceidæ: *Gymnura* only.
- Galeopithecidæ, "flying lemurs."

Order Cheiroptera, bats.

Order Primates.
- All but man, the baboons and a few ground monkeys.

Only excepted orders: Monotremata, Cetacea, Sirenia.

Bionomic Classification

Wall and Rock Climbers.—The classification of scansorial animals from the standpoint of their adaptation groups them into three subdivisions, of which the first are the wall and rock climbers. These are not necessarily tree-inhabiting at all, but are, like the gecko lizards, well suited for climbing on the walls of buildings as well as on similar surfaces in nature. The geckoes (see Fig. 77) are, however, a very old and widely distributed group, and the range of their individual adaptation is great, hence it may well be that their scansorial adaptation is after all a response to arboreal life, and that the peculiar structure of their climbing organs rendered sub-

sequent rock-climbing possible. Among mammals there is a genus of flying squirrels limited to high altitudes at Gilgit and perhaps in Thibet, and thought to live on rocks, perhaps among precipices (Beddard). Here, again, we have a form whose ancestry may have been arboreal, but if not, it would afford an interesting instance of volant adaptation without an intermediate arboreal habitat.

Terrestrio-arboreal Forms.—The second category, the terrestrio-arboreal, embraces a number of carnivores, rodents, and insectivores which, while capable of climbing, nevertheless are still perfectly at home upon the ground beneath the trees. They may nest in the trees with more or less extensive terrestrial excursions during the daytime, or they may climb for food and live on the earth unless impelled by hunger. Their climbing adaptations are not very marked.

Arboreal Forms.—Still a third group embraces the wholly arboreal types, creatures which make the trees their home, and while some occasionally descend to the ground as in certain primates (gibbon), their terrestrial progression may be slow and laborious compared with that in their true habitat. Arboreal forms, according to their mode of locomotion, may be grouped in the following subdivisions:

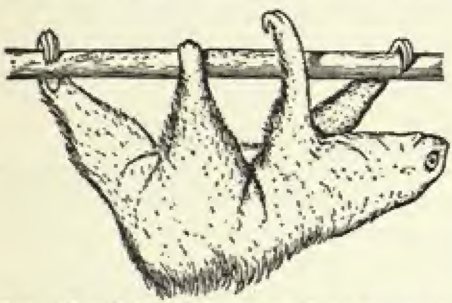

FIG. 65.—Sloth, *Cholœpus*, walking suspended from a branch. (After H. Allen.)

1. *Branch runners*, like the squirrels, marsupials, lemurs, and chameleons, which live and progress on all fours on the upper surface of the branches. The group embraces, nevertheless, some instances of very perfect arboreal adaptation, as the great majority of tree-dwellers are here included.

2. *Forms suspended beneath branches.* The sloths (Fig. 65), for instance, are so constituted that they cannot walk upon the branches but rest and move suspended from them by the powerful recurved claws of all four limbs. Sometimes when quiescent, if a convenient branch lie sufficiently near, the sloth may rest his back on it and relax the hold of one or more of his feet, but the inverted position is rarely reversed. On the ground the animal

progresses with the utmost difficulty. The bats should perhaps also be included under this head, as they rest suspended by the hind limbs, head down. The same position of rest is assumed by the so-called flying lemur, *Galeopithecus,* really not a lemur at all but an insectivore (see page 317).

3. *Forms swinging by the fore limbs* (brachiators, Gr. βραχίων, arm). These forms show a very remarkable method of progression by means of the fore limbs, swinging with great speed and accuracy from limb to limb and from tree to tree. The hind limbs are comparable to those of the tree-dwelling marsupials and the creatures rest and progress on the tops of the branches at times, although the fore limbs are almost the sole organs of more rapid locomotion. Here belong many of the primates, more especially the great or manlike apes, and our pre-human ancestors.

Modifications

Body.—Climbing adaptation, as in the other lines of adaptive radiation, implies certain body modifications as well as those of limbs. Body contour is of little moment in climbing, but strengthening of chest and ribs and of shoulder and hip girdles is of importance. Nevertheless, in thoroughly arboreal types the section of the thorax anteriorly is subcircular, and the ribs are much curved, in contrast with the compressed thorax and flat anterior ribs of quadrupedal running types (Anthony). The ribs, especially in the sloths, are numerous and afford ample support to the contained viscera in their inverted position. The dorso-lumbar series of vertebræ is often elongated, especially in the tree-sloths of the genus *Cholœpus* (Fig. 66), where the number has apparently been increased from about nineteen (normal for the order) to from twenty-five to twenty-seven as a response to arboreal need. The same is true of other forms. *Capromys,* an arboreal rodent, has twenty-three as compared with the normal nineteen, and *Dendrohyrax,* the only arboreal ungulate now alive, has six more than its terrestrial, hoofed relatives.

Limb Girdles.—The shoulder girdle especially is strong in that both elements, the clavicles and scapulæ, are well developed, although in terrestrial types the clavicles tend to diminish, even in closely related forms, and may entirely disappear as in cursorial quadrupedal forms. The fore-and-aft swing of the limb of a deer or horse would be distinctly limited by a clavicle, but in a climbing

type whose arms are subjected to much more varied and violent strains the clavicle is very essential, as it withstands the compression of the powerful breast muscles. The scapula is also well developed, but not exceptionally so.

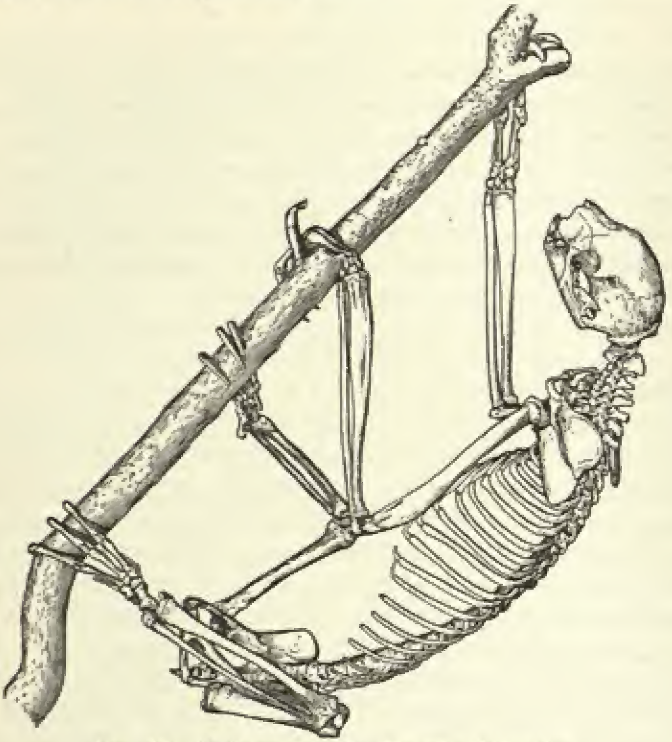

FIG. 66.—Skeleton of sloth, *Cholæpus didactylus.*

Pelvic Girdle.—The ilium or hip-bone especially shows modification in such types as the sloths and primates, as it is broadened out as a support for the viscera. This is markedly true of the sloths, whose inverted posture necessitates additional support, since the mesenteries or membranes which sling the intestine to the dorsal wall lose much of their efficiency when the body is erect or inverted.

Limbs.—In contrast with the cursorial types, it is the proximal limb segments which now elongate, especially in the suspended and brachiating forms, those of the sloths again being very long, while in the great apes the relative length bears a direct ratio to the creature's climbing powers, reaching the extreme in the gibbons

(*Hylobates*) whose arms are so long that the knuckles of the hand touch the ground when the animal stands erect. The progress of the gibbon from branch to branch and tree to tree is remarkable (see page 649 and Pl. XXVII). Climbing forms are generally plantigrade, some of the raccoons secondarily so. In certain lemurs (*Tarsius*, see Fig. 244; *Galago*) the tarsus may be elongate, but this is probably due to the fact that the creatures leap as well as climb, and the elongation of this segment is a response to the former need rather than to the latter.

Feet.—The feet of arboreal animals may be either prehensile, that is, grasping, with more or less opposable digits, or non-prehensile. In the *non-prehensile type* the claws may be well developed as in the squirrels or the cats, giving a fairly tenacious hold. In the Canada tree-porcupine (*Erethizon*) the plantigrade feet are armed with long curved claws, in addition to which the soles bear spines and tubercles which aid in climbing.

Adhesive pads either on the tips of the digits or on the soles of the feet occur in several isolated instances, such as the tree-frogs, geckoes, and *Dendrohyrax* among mammals. The frogs are aided by a sticky secretion of their pads. "Tree-frogs, when hopping on to a vertical plane of clean glass, slide down a little, probably until the secretion stiffens, or dries into greater consistency. . . . Wet leaves or moist glass-walls afford no hold. The adhesion of these frogs is assisted in most cases by their soft and moist bellies, just as a dead frog will stick to a pane of glass" (Gadow).

The geckoes, by means of their adhesive digits, climb up absolutely smooth and vertical surfaces, or, back downward, along a whitewashed ceiling. The apparatus, Gadow says, is complicated in its minute detail, but very simple in principle. The adhesion is effected not by sticky matter, but by small and numerous vacua.

Dendrohyrax, the tree-hyrax, is allied to the coney of Scripture. The tree-hyraxes frequent the trunk and larger branches of trees, sleeping in holes high up in the big trees, especially, according to Roosevelt's observations, the cedars. The adhesive organs have been described by G. E. Dobson, who says that these animals are enabled to climb perpendicular walls and trees without the use of claws. The thickly padded tuberculated soles are drawn up by certain flexor muscles, thus leaving a partial vacuum by means of which the animal retains its hold.

The primitive type of prehensile foot has been developed in the

two great mammalian groups, that of the marsupial being represented by the opossum (*Marmosa*, Fig. 39,A), and that of the early placentals by the creodonts, the archaic flesh-eating mammals (see Chapter XXXII), the foot of which has been shown to be a terrestrial modification of a grasping type.

Feet of the *prehensile type* are found to-day in the marsupials and primates. In the former group it is the hallux (see Fig. 39) or great toe which is offset so as to oppose the fourth digit, the second and third being bound together in a common integument (syndactyly, see page 249) and so slender that their combined strength about equals that of the outermost or fifth digit. In marsupials which have become terrestrial the offset great toe has become vestigial or may entirely have disappeared, as in the kangaroos (see Fig. 39,B). In the primates, while the foot is perhaps most apt to show this opposable first digit, it also exists in the hand, although it is nowhere developed to the degree shown in mankind, wherein the final perfection of the hand as an organ of prehension has developed since its release from the necessity of arboreal locomotion.

Syndactyly (Gr. σύν, together, and δάκτυλος, digit) has already been referred to as occurring in the marsupials, and even such as are no longer tree-inhabiting, like the kangaroo, still exhibit this feature in unreduced condition. It doubtless arose primarily, however, as an arboreal adaptation. The koala shows a rather remarkable modification for climbing, for the foot has a long, widely offset, clawless great toe, syndactylous second and third toes, which are clawed, and powerful clawed fourth and fifth toes, the former being the longer. The hand, on the contrary, has five subequal digits, all of which bear sharp claws; but two digits, numbers 1 and 2, oppose the other three. Its clinging powers are so great that even death will not dislodge the creature from the tree in which it is shot.

Among reptiles, the true African chameleons (*Chamæleon*, see Fig. 67) exhibit remarkable syndactyly, as it extends to both fore and hind feet. On the hand the first three fingers form the inner bundle and are opposed to the outer two which are likewise syndactylously bound. The foot is similar but reversed, in that the inner bundle contains two, the outer one three digits. These very admirable grasping organs are supplemented by a prehensile tail, so that the creature is very firmly anchored in position, which is

rendered necessary perhaps in part by its method of securing insect prey by the unerring aim of the enormously extensile tongue.

In the so-called scansorial birds such as the parrots, woodpeckers, and the like, the outermost toe has been rotated backward in such a way that it and the hallux oppose the second and third toes, the fifth, as in all birds, being absent. This gives a very firm grasp

FIG. 67.—Chameleon, showing syndactylous hands and feet, and prehensile tail. 2, head with partly protruded tongue; 3, head of horned chameleon, from above.

for the actual grip of a branch as in the parrots or, reinforced by strong claws, enables the animal to cling to the roughened bark of a tree trunk. In the parrots, woodpeckers, and cuckoos the rotation of the outer toe is permanent and the foot is called zygodactylous (Gr. ζυγόν, yoke); certain others, owls, etc., may turn it backward or not at will (see Fig. 68).

While arboreal forms usually have need of all of their digits, occasionally one sees *digital reduction*. The foot of the koala, with syndactylous second and third toes, functions as four-toed, even

though consisting structurally of five; certain of the primates (lemurs), on the other hand, some of which resemble the koala superficially very much, have actually lost the second digit so that the opposability of the first in grasping a limb is unimpeded. In the lemur (potto, etc.), the fourth digit is the largest as in the koala. Digital reduction is also seen in the tree-sloths, the two-toed sloth *Cholœpus* (Figs. 65, 66) having but two in the hand and three in the foot, while in the three-toed sloth *Bradypus* there are three in each, and the hand and foot are both somewhat elongated, especially in the powerful hook-like claws which, like the feet of the koala, retain their grip on the bough even after the animal has been shot.

Fig. 68.—Foot of a woodpecker, *Picus viridicanus*, showing fourth toe reversed for grasping. (After Haacke, from Abel.)

Tail.—The tail may be prehensile or not as in the case of the feet. If non-prehensile, there are ectodermal spines or scales on the under side, as in the flying squirrel *Anomalurus*, which prevent the animal from slipping down. The same effect is produced in the woodpecker by stiff spiny feathers which are braced against the tree trunk to which the creature clings. The posture is familiar, and enables the bird to drill into the wood for the grubs upon which it feeds, or to excavate cavities for its nest or for the storage of food.

Prehensile tails are found in a number of unrelated instances, as, for example, the chameleon lizards which have been mentioned, the opossums, the tamandua which is one of the anteaters, and certain of the New World monkeys (Cebidæ) such as the spider monkey (see Fig. 245), the howlers, and the capuchins. Where the prehensile powers are well developed the tail is naked on the under surface near the tip. One of the most perfectly adapted of these forms is the spider monkey, *Ateles*, in which the tail is highly prehensile and functions as a "fifth hand." Perhaps as a correlation with this excellent grasping organ the real hands have lost the thumb, but the four long digits which remain form a splendid hook-like device for suspending the body. Not all South American monkeys have a prehensile tail; on the other hand, none of the Old World forms do, so that its presence is diagnostic of a NewWorld ape.

Other Accessory Organs.—Other accessory climbing organs might be mentioned, such as the parrot's beak and the spines and

tubercles which are sometimes developed on the fore arm in certain lemurs (*Hapalemur griseus* male and upon the lower end of the ankle in *Galago garnetti*). In *Lemur catta* there is a patch of hardened skin on the fore arm which projects to a large extent and has been called a climbing organ, although it lacks the recurved spines; both this and the spiny patches of *Hapalemur* and *Galago* have glands connected with them, the function of which is doubtful.

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CHAPTER XXII

VOLANT ADAPTATION

Next to water as a moulding environment comes the air, for the creature which inhabits either is surrounded on all sides by a homogeneous medium so that it becomes uniformly and beautifully modified to offer the least possible resistance to the attainment of speed. Water-inhabiting forms, however, whether primarily or secondarily adapted, may become so thoroughly at home that in the latter group no evidence of their former habitat is outwardly visible. Aërial creatures, on the contrary, are never exclusively such and must return to the trees or earth or sea when they wish to rest. Hence their adaptation is always a double one and as a consequence cannot reach the extreme of specialization of water-borne types.

Classification of Flight

Passive or Gliding Flight.—Flight is of two sorts: first, passive or gliding flight, in which, with the exception of the fishes, the creature merely takes an initial leap from a high point and, held up by certain sustaining organs and impelled by gravity, glides to a lower level, sometimes covering a horizontal distance of many yards. Aside from the initial impetus there is no locomotive force other than gravity, so that the flight is comparable to a gliding airplane without engine power.

True Flight.—True flight, on the contrary, implies power, so that there is sustained movement through the air, whether the flight be brief like that of a domestic hen or supported on the tireless pinions of an albatross. True flight has evolved three times among vertebrates: in the reptilian pterodactyls, the birds, and the bats. Whether flying fishes should be included is a much disputed question. True flyers may move the wings with varying degrees of rapidity from the extreme speed of a humming-bird's wing to the measured cadence of a winging crow. Many birds (and doubtless some of the ancient pterosaurs) also sail or soar on apparently motionless wings for hours at a time after having gained their altitude by a flapping rise. They are in reality gradually

descending in a great spiral, although by taking advantage of the shifting currents of air they may retain their elevation with little apparent expenditure of energy.

An extreme adaptation of this last method is that seen in the albatross, whose majestic flight is thus described by Hutton: "With outstretched, motionless wings he sails over the surface of the sea, now rising high in the air, now with a bold sweep, and wings inclined at an angle with the horizon, descending until the tip of the lower one all but touches the crests of the waves as he skims over them. Suddenly he sees something floating on the water and prepares to alight; but how changed he now is from the noble bird but a moment before all grace and symmetry. He raises his wings, his head goes back, and his back goes in; down drop two enormous webbed feet straddled out to their full extent, and with a hoarse croak, between the cry of a raven and that of a sheep, he falls 'souse' into the water. Here he is at home again, breasting the waves like a cork. Presently he stretches out his neck, and with great exertion of his wings runs along the top of the water for seventy or eighty yards, until, at last, having got sufficient impetus, he tucks up his legs and is once more fairly launched in the air."

The flight of the albatross seems to be sustained on motionless wings and yet it will follow the wake of a ship with all of the apparent ease with which a school of porpoises precedes her bow. In the latter, when viewed from above, there are no *visible* propelling movements except at long intervals when a few rather vigorous dorso-ventral undulations of the tail are seen which, however, do not seem to accelerate the creature's speed appreciably. A closer view, especially if one be more nearly on a level with the water, shows the tail to be in rapid but minute vibration all the time, and this intense movement is sufficient to keep the creature ahead of a 39-knot destroyer (the record) and even this does not seem to be the limit of its speed. The progress of the albatross is apparently analogous, for, as Moseley says, "I believe that albatrosses move their wings much oftener than is suspected. They often have the appearance of soaring for long periods after a ship without flapping their wings at all, but if they be very closely watched, very short but extremely quick motions of the wings may be detected. The appearance is rather as if the body of the bird dropped a very short distance and rose again. The movements cannot be

seen at all unless the bird is exactly on a level with the eye. A very quick stroke, carried even through a very short arc, can of course supply a large store of fresh momentum."

Doubtless the albatross takes advantage of every shift in the breeze, which is made up of a complex of varying air currents, tilting this or that wing to gain whatever lifting power the air can give. That this "jockeying" of the air currents is a very great aid is attested by the fact that on a calm day the albatross cannot sail, but must flap heavily to sustain itself in flight. It is analogous to man's flight in an engineless glider.

Modifications

Body contour in volant animals has been emphasized and is second only to that of the purely aquatic forms in its degree of perfection for the lessening of resistance.

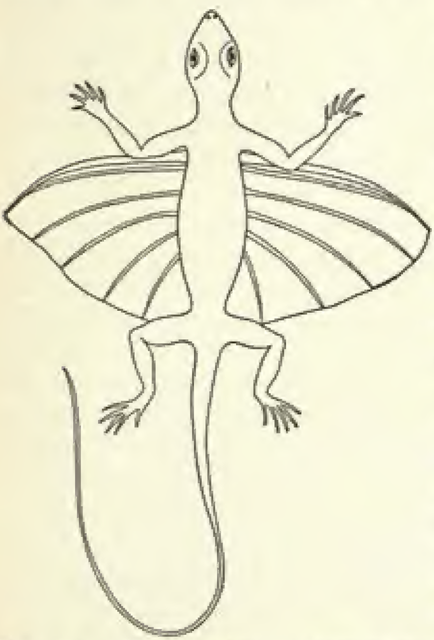


Fig. 69.—"Flying dragon," *Draco volans*. (After Lull.)

Sustaining Surface.—The sustaining surface is primitively, except in the fishes, a fold or series of folds of the skin known as the *patagium* (Lat. *patagium*, an edge or border). This may be supported in various ways, but with one exception, in the little lizards (*Draco* spp.) which inhabit the Indo-Malayan region, the limbs form the chief supporting agents. In the "flying dragons," *Draco* (Fig. 69), just mentioned, the body is depressed and the sides extend outward into a pair of large, wing-like membranes, supported by five or six elongated ribs. The entire device can be folded like a fan against the sides of the body when not in use. The soaring powers are not very great but when resting among the luxuriant foliage of their habitat

the animals are said to resemble butterflies in their habit of opening and closing the wings.

Most soaring mammals have the patagium supported between the fore and hind limbs, and sometimes the skin-fold extends in front of the fore limb to the neck and again between the hind limbs and the tail. Perhaps the extreme of development may be seen in *Galeopithecus* (Fig. 70), the so-called "flying lemur," for here the patagium extends from the sides of the neck to the tip of the tail, even including the digits, which are webbed as though for aquatic life (see page 331).

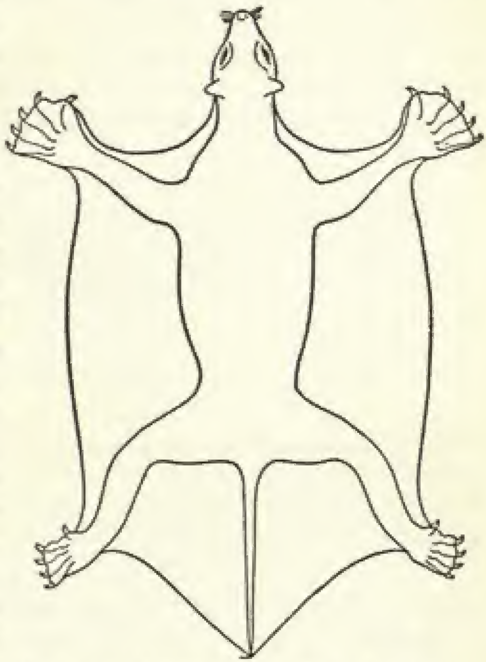


Fig. 70.—*Galeopithecus volans*. (After Lull, modified from Wood.)

Where the patagium is supported mainly by the elongated fore limbs and their digits, true flight ensues as in the pterosaurs, wherein the enormously elongated outer finger sustains over half the membrane, and in the bats, whose second, third, fourth, and fifth digits perform a like function, the first alone being free. In both groups the membrane extends from the arm to the sides of the body and also to the front of the hind limb. An interfemoral membrane, which, however, may have existed, has not been demonstrated in the pterosaurs but is variably present in bats.

Feathers are structures which are absolutely diagnostic of birds, since no other group of animals has developed them, and indeed their complexity is such that there is little likelihood of nature's repeating herself in their evolution as she has done many times in that of simpler structures. Birds have traces of patagia in front of and behind the arm which may have had a very adequate sup-

porting function before the feathers usurped their place; but in all known birds the main buoyancy is provided by the broad vanes of the remiges (supporting feathers) of the wing and the rectrices (steering feathers) of the tail which collectively form the most perfect device imaginable, except, perhaps, the insect's wing.

The feather (see Fig. 71) has been called "nature's masterpiece," and while simply a modified reptilian scale, has reached a complexity so great that its component parts may be counted by the hundreds of thousands. It is thus described by Evans: The feather consists of a quill or calamus and the rhachis or shaft. On the rhachis a double series of barbs are developed, carrying a similar double series of barbules, the barbules again giving rise to barbicels,

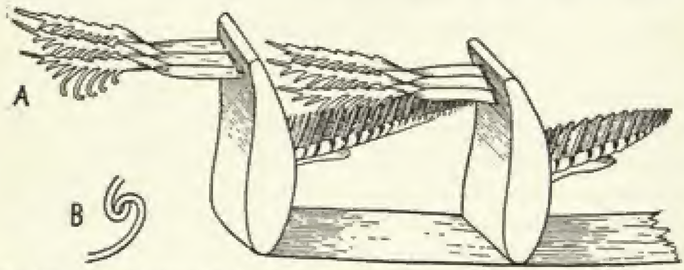


Fig. 71.—Structure of a feather. A, small portion of feather, with pieces of two barbs, each having to the left three distal barbules, and to the right a number of proximal barbules, many of them belonging to adjacent barbs; B, hooklet of distal barbule, interlocking with flange of proximal barbule. (After Pycraft, from Parker and Haswell.)

which in the distal rows usually terminate in hooklets. These catch in the folded margins of the next proximal row, thus producing a firm surface. Each flight feather, therefore, forms a membrane-like supporting device, the several feathers of the wings being collectively sufficient to maintain the bird in the air even when a few at a time are lost as during the moulting season.

Wing.—The wing, as we have seen, has been three times evolved, twice with patagia and once with feathers. A comparison of the three types is of interest, beginning with the *bat wing* (see Fig. 13,F), which is the latest in time and hence naturally the least modified. Here the humerus is well developed, the radius long and curved, and the ulna, from loss of general utility, vestigial as in cursorial types. The pollex or thumb is always free and clawed

for crawling and climbing. In the smaller bats, Microcheiroptera (Fig. 83,A), the second finger, although distinct, is not free from the third but is attached to it distally, the two combining to support the anterior margin of the wing. The fourth and fifth digits are well developed. In the Megacheiroptera (Fig. 83,B), or fruit bats, the second digit is independent of the third and bears a claw like the first.

In the *pterodactyl wing* (see Fig. 13,D) the radius and ulna are more nearly equal, the former being somewhat smaller. The next segment consists of a very heavy fourth metacarpal, bearing the great wing-finger, and three extremely slender metacarpals supporting the first, second, and third digits, which are small but free and clawed. There is also the bone known as the "pteroid" which lies in front of the fore arm and is directed inward toward the shoulder. It is supposed to have supported the anterior margin of a small prepatagium which lay in front of the arm from the wrist to the neck (see Fig. 79). The single wing-finger, presumably the fourth, is huge and formed the entire anterior support of the patagium beyond the wrist. One curious feature of the pterodactyl wing lies in the position of the principal joint, the wing being flexed between metacarpal and proximal phalanx, rather than at the wrist as in birds and bats.

The *bird wing* (see Fig. 13,E) is the most specialized of all, for here not only are the digits reduced to three, but these are more or less fused together so that, with rare exceptions, their sole function is that of flight. In all modern birds, therefore, there are three unequally developed metacarpals which are firmly coössified. The digits are represented by one or rarely two thumb phalanges which support the so-called bastard quills, while the second digit, which is much the largest, bears two phalanges, and the third, one. Claws are sometimes borne on the first and second digits of modern birds, while *Archæornis* (Fig. 80,A), a reptilian bird of the Jurassic, had a claw on each of the three free fingers. The alar or wing expanse is provided by the feathers, since the patagium, as we have seen, is vestigial. These feathers, known as remiges, are borne upon the hand (primaries), and on the arm (secondaries). Overlying their basal portion are several rows of coverts, protective feathers known as major, median, minor, and marginal. The importance of the wing coverts lies in the fact that they close the interstices between the quills of the flight feathers and give the wing a continuous area

to oppose the buoyancy of the air (see Fig. 72). Birds have an advantage over both bat and pterodactyl in that lost or injured feathers are renewed, while serious injury to the patagium may impair its owner's powers of flight for life.

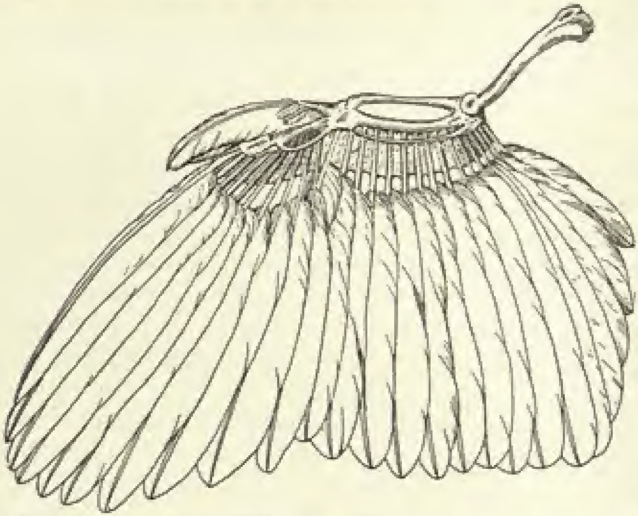


FIG. 72.—Wing of pheasant, showing the two "bastard quills" borne on the first digit, the ten primaries on the hand, and the sixteen secondaries on the fore arm. (After Heilmann.)

Pneumatic Bones.—Hollow, air-filled bones are found in the birds and pterodactyls and in many ways they show a remarkable community of design. For instance, there is in the humerus of both pterodactyl and bird a foramen for communication between the respiratory organs and the cavity of the bone, but that is not so remarkable as the fact that in each instance the foramina correspond in position, form, and size, and that they are not one large hole, but in each case a reticulation of small perforations, one beyond the other. So far as our knowledge goes, pneumaticity seems to have been universal among pterosaurs, but there are no degenerate or flightless pterosaurs known. On the other hand, birds do not all possess it in equal degree for, as one would expect, it is absent from the Ratitæ, nor is it developed equally in all birds with flight. Coupled with the pneumaticity in birds is a remarkable development of air sacs, principally in the abdomen, but in other portions of the body as well. These serve not only to lighten the

specific gravity of the bird, but also to aid in respiration, for the lungs of birds are inelastic and do not hang freely in the body cavity as they do in mammals, but, by means of the abdominal sacs, air is drawn *through* them, not merely into them. Hence there is no unused portion of the lung containing residual air, as in mammals, and respiration is much more effectively accomplished. This is necessary, for with the rapid flight there is a high expenditure of energy, and the respiratory and nutritive organs and those of circulation need to be ample and efficient to meet the demand upon them.

Sternum and Shoulder Girdle.—Not only is the sternum or breast-bone well developed in creatures with true flight, but it bears a median keel or carina for the origin of the pectoral muscles which wield the wings. To resist the contractile force of these muscles the shoulder girdle is made very rigid by the development of the clavicles and, in the birds, of the heavy pillar-like coracoids as well. Coracoids are lacking in the bats, and clavicles in the pterosaurs, but in birds both elements are present. In the pre-Cretaceous pterosaurs the scapula is saber-shaped and united to the coracoids at an angle of less than 90°, exactly as in carinate birds. The Cretaceous pterodactyls differ, however, in that the scapulæ, while articulating at right angles with the coracoids, are directed toward the vertebræ, uniting with their neural arches. In the great pterosaur *Pteranodon* (Fig. 79) the scapula articulates with the coalesced spines of several coössified vertebræ which constitute the so-called notarium, the whole mechanism being comparable to the pelvic arch although on a much larger scale.

In the flying (carinate) birds the scapula and coracoid are united by an articulation; in the flightless Ratitæ, on the other hand, they are firmly coössified, and form an angle with one another greater than a right angle. In the Ratitæ, as the name implies (Lat. *ratis*, raft) the sternum is raft-like, and bears no keel.

Brain and Sense Organs.—True flight implies a good brain and the perfection of certain sense organs which, as we have seen, are developed in direct ratio with the locomotive powers of any animal. The brains of bird and pterosaur are curiously alike in that each has broad, well developed hemispheres (cerebrum) which touch the cerebellum behind, and the optic lobes are much enlarged.

Both birds and pterodactyls were well endowed with visual organs, the eyes in each case being large and having the so-called

sclerotic plates, structures which are rarely elsewhere present except in certain reptiles (dinosaurs, ichthyosaurs, mosasaurs, etc.). Their function may be to resist variable pressure and also to aid in the rapid focussing which is of vital necessity in bird and pterodactyl. The bats, while reputedly blind, often have very good vision, especially during twilight. They also have a most marvellously developed tactile sense, which does not seem to need actual contact for the discernment of approaching objects. The remarkable ears and facial appendages of certain bats are the principal seat of this sense and the patagia and interfemoral membrane are also highly sensitive.

Flying Vertebrates

Fishes.—There are enumerated several genera of flying fishes, each of which represents a separate volant adaptation. Of these

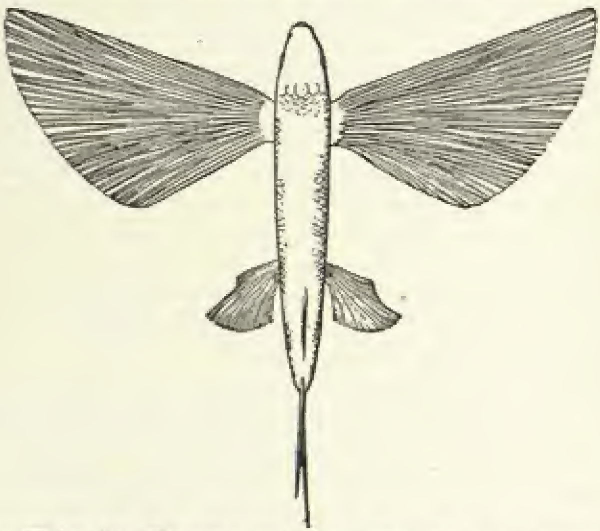


Fig. 73.—Flying fish, *Exocœtus spilopterus.* (From British Museum Guide to Flight.)

the first to be mentioned are the several species of the genus *Exocœtus* (Fig. 73), allied to the skippers and garfish, which live in all tropical and subtropical seas where they fly in shoals in their efforts to escape the relentless tunny and albicore. These flying fishes are trim-built creatures with large pectoral fins, which are the main organs of flight, and variably developed but much smaller

pelvics. The lower lobe of the tail is invariably the longer and aids in giving the final impetus to the fish as it leaves the water and also in accelerating its speed if in the course of its flight it comes near enough to the surface of the sea. The length of flight is said to vary up to 200 or 300 yards and it is sometimes sufficiently high to strand the creature on the deck of an ocean-going craft. Whether the flight of *Exocœtus* is true flight or merely a soar is a much disputed question and the evidence, briefly summarized, is as follows:

The wing expanse is hardly sufficient for such extended soaring. The wings (pectoral fins) do vibrate, but whether due to muscular effort or to friction, as a flag is flapped in the wind, is not clear. The muscular development seems insufficient for true flight, but on the other hand it is more highly developed than in allied non-flying fishes. It may well be that while true flight as such does not exist among fishes, rapid wing vibration insufficient in itself to support or drive the animal may aid in maintaining or prolonging a soaring flight of which the main propulsive effort is acquired by the tail before leaving the water. At all events, their flight is remarkable and the creatures are one of the most interesting features of the storied tropical seas.

The various species of *Dactylopterus* (Fig. 74) are known as the flying gurnets and while the flight is by no means as sustained as in *Exocœtus*, of the former fishes Moseley writes: "I have distinctly seen species of flying gurnets move their wings rapidly during their flight . . . especially in the case of a small species of *Dactylopterus* with beautifully colored wings, which inhabits the Sargasso Sea." Moseley likens the flight of the gurnets to that of grasshoppers.

There is an African flying fish found in the Congo and Niger rivers—*Pantodon*, a form but three or four inches long—which leaps out of water and flutters through the air for some distance. Still another flying type is *Gastropelecus*, a small, compressed fish with long and curved but not particularly large pectoral fins, which occurs in the rivers of British Guiana. It skims along the surface of the water for 40 feet or more, beating the water with its pectoral fins. Then it leaves the water for a distance of five to ten feet and when exhausted falls sideways into the water again (Eigenmann). *Pegasus volitans*, a little fish found along the coasts of Japan, China, India, and Australia, skims a short distance above the surface of the water by means of its broad pectoral fins.

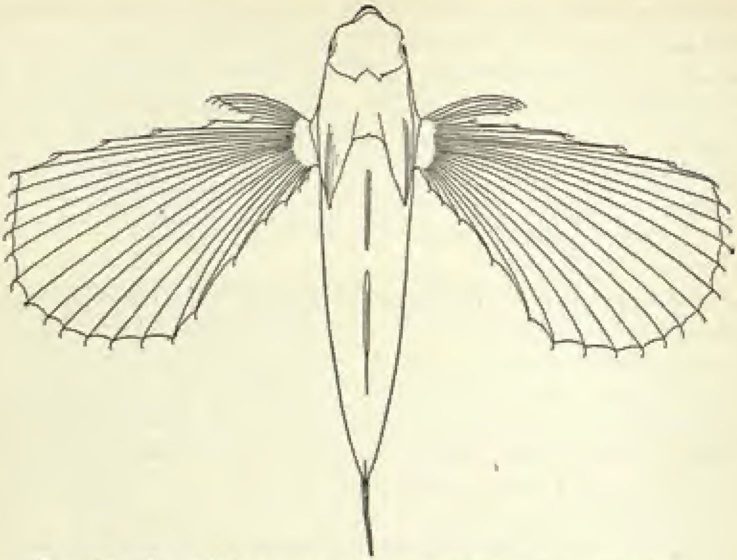


FIG. 74.—Flying fish, gurnet, *Dactylopterus volitans.* (After Lull.)

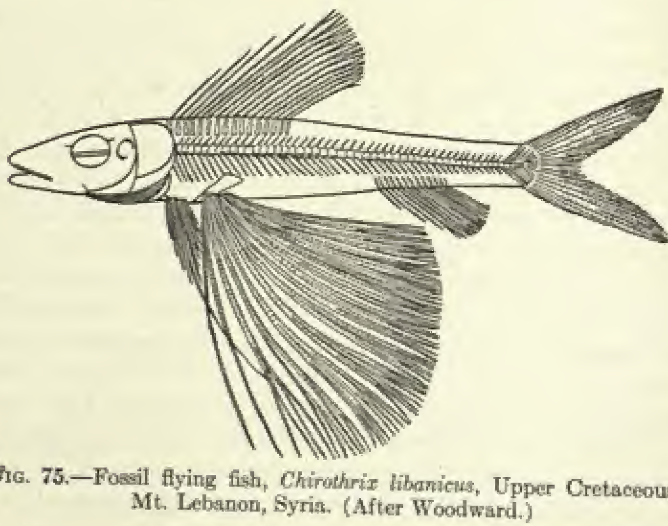


FIG. 75.—Fossil flying fish, *Chirothrix libanicus,* Upper Cretaceous Mt. Lebanon, Syria. (After Woodward.)

Several extinct forms have been described as "flying fishes." These are: *Dollopterus* from the Middle Trias (Upper Muschelkalk) of Jena, *Thoracopterus* and *Gigantopterus* from the Upper Trias of Austria, *Exocœtoides* and *Chirothrix* (Fig. 75) of the Upper Cretaceous of Mt. Lebanon, Syria. The last mentioned is of particular interest on account of the huge size of the pectoral fins, which seem to imply powers of flight fully equal to those of the living *Exocœtus* and *Dactylopterus*. We have therefore among fishes no fewer than ten separate adaptations to aërial conditions, one or two, possibly three of which approach very near to, if they have not attained, true flight.

FIG. 76.—Flying frog, *Rhacophorus reinhardtii* (After Duméril and Bibron, from Lull.)

Amphibia.—The only volant adaptation among amphibia is that of the tree-frog, *Rhacophorus* (Fig. 76), whose webbed feet sustain it in the prolonged leaps to which it is addicted. This genus includes a large number of species in the Oriental realm, especially in Borneo. The digits terminate in adhesive pads, in common with those of other tree-frogs, and are connected by web-like expansions of the skin. There are also rudiments of patagia in front of and behind the arms. In *Rhacophorus pardalis* the total alar expanse is about three square inches, which would imply rather feeble gliding powers.

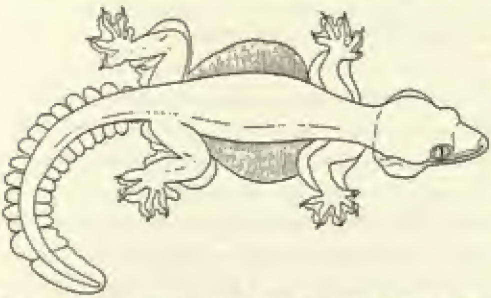


FIG. 77.—Lizard, *Ptychozoön homalocephalum*. (After Duméril and Bibron, from Lull.)

Reptilia.—Lizards include at least two genera and several species of gliding forms, of which the most remarkable is the flying dragon, *Draco*, already referred to (page 316, Fig. 69), in which the patagium is supported by a number of extended ribs. They occur principally in the Malay Peninsula and Archipelago and average some eight to ten inches in length.

Ptychozoön (Fig. 77) is the flying or fringed gecko of the Malay countries, which is bedecked with lateral expansions of skin along the sides of the neck, body, tail, and limbs, and between the toes. While these may aid in breaking the creature's fall, they may also, coupled with the color, serve a cryptic function and render the animal less conspicuous against the bark of the tree upon which it rests.

Several so-called flying snakes are recorded, such as *Chrysopelea*, the flying snake of Borneo, which descends obliquely through the air, its body rigid, and the ventral side concave to sustain the creature in its fall.

The pterodactyls or flying dragons of the Mesozoic were a very remarkable group of reptiles whose first recorded appearance

FIG. 78.—Pterodactyl, *Rhamphorhynchus phyllurus*. (After Lull.) At lower right, vertical rudder-like expansion at end of tail.

is in rocks of the Rhætic or uppermost Triassic period. They range through the Jurassic and on into the Upper Cretaceous, when they become extinct through racial death. They were undoubtedly akin to the birds, but that simply means, in all probability, derivation from a common, possibly Permian ancestry; nevertheless the two groups show a number of highly comparable, homoplastic characters, some of which have already been referred to. The remarkable thing is that, like the turtles, they first appear fully developed and characteristic of their order, with no record thus far discovered of their antecedent evolution, and the subsequent changes are mainly increase in size, perfection of the shoulder girdle articulation (see page 321) and loss of tail and of teeth. In size

they range from that of a sparrow to the mightiest of nature's airplanes, for the replica of the late Cretaceous *Pteranodon* (see Fig. 79) mounted at Yale measures 13 feet 6 inches in alar expanse and Eaton is authority for the statement that at least one individual, judging from the relative proportions of the bones which have been preserved, had an estimated breadth of 26 feet 9 inches from tip to tip. The pterodactyls possessed true flight, which in those from the Kansas chalk must have been sustained, as their remains are found in association with marine reptiles, fishes, and invertebrates, apparently far from the ancient shore. Three of the principal horizons whence these pterodactyls come, the Lias of Lyme Regis of England, the lithographic limestone (Upper Jurassic) of Bavaria, and the Kansas chalk, are all marine in origin, which is also true of the source of the Mesozoic birds. It

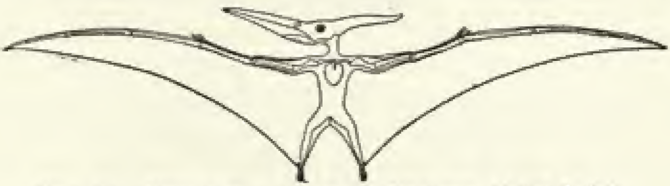


FIG. 79.—Pterodactyl, *Pteranodon longiceps*. (After Lull.)

is highly probable therefore that in each instance we have not as yet knowledge of the great bulk of the group, but only of a few of aberrant habits and adaptation.

Birds.—The birds in all probability include but a single evolution to aërial life, although certain excellent authorities "believe more or less firmly that possibly birds had not one, but two points of origin, and feel that if we could follow back their lines of descent we should find that the ostriches came from one and the birds of flight from another" (Lucas). If this be true, the ratite or ostrich group as a whole, with a single exception (tinamou), have degenerated and lost the power of flight, although an examination of the skull and skeleton shows them to have been descended from flying normal birds; whereas in the carinate or flying birds loss of flight, while it has occurred (flightless rail, penguin, dodo, etc.), is relatively extremely rare. Flightless pterosaurs and bats, on the other hand, are inconceivable, as their flight mechanism involves the hind limbs which have, as a consequence, largely lost their terrestrial locomotion function; whereas birds, being double adapted.

can lose their flying powers and still progress easily on the ground or in the water, as their legs are not thus involved.

Birds first appear in time in the Upper Jurassic (Solenhofen limestone) long after the initial record of the pterodactyls. These first birds, of which but two or three specimens have been recovered, are known as *Archæopteryx* and *Archæornis* (see Fig. 80

FIG. 80.—Reptilian bird, *Archæopteryx* (A), compared with pigeon, *Columba livia* (B). (After Lull.)

and Pl. XIV) and are so reptile-like that were it not for the preserved feathers it is doubtful whether they could be surely proved to have been birds. The reptilian traits are teeth, free clawed fingers in the hand, feeble breast-bone, abdominal ribs, etc. For a discussion of the origin of birds, see Chapter XXXI.

The perfection of aërial adaptation among birds is superlative, as records will show compared with those attained by the man-

evolved airplane. With regard to speed, the record is held by a house-swallow (*Chelidon urbica*) which flew from Ghent to Antwerp, a distance of 32 miles, in $12\frac{1}{2}$ minutes, an average speed of 153 miles an hour. Some bird speeds as compared with those of airplanes are given as follows, the figures being in miles per hour: white storks at 4200 feet altitude, 48; mallard, 50; rook, 45; gannet, 48; geese, 55; lapwing, 40 to 45; golden plover pursued, 60. Swifts (*Apus apus*) at 6000 feet above Mosul easily passed and circled an airplane doing 68 miles, and a lammergeier made 110 while nosediving to escape a plane. For distance, the record is held by an albatross in the Brown University Museum, which flew 3150 miles in 12 days—probably more, as it rarely flies in a straight line. The weight of this bird was 18 pounds, wing spread 11 feet 6 inches, area 7 square feet. As regards height, the great vulture rises from 7000 to 15,000 feet and Humboldt, a very accurate observer, saw a condor hovering above Mt. Chimborazo, whose summit soars 20,498 feet into the blue.

Mammals.—Among the mammals there are upward of thirteen separate volant adaptations, one of which, that of the bats, attained the power of true flight. Among the flying forms the first to be mentioned are the *marsupials*, of which the flying phalangers include several unrelated species: *Petaurus* spp., *Petauroides volans*, and *Acrobates pygmæus*. These are characterized alike by having a well developed skin fold along the sides of the body between fore and hind limbs, and a feebly developed one in front of the fore leg. In each genus the flying form is especially related to a separate type of non-flying phalanger.

In *Petauroides* the flying membrane extends from wrist to ankle, but is very narrow along the distal segment of each limb. The tail is very bushy except for its prehensile tip, which is naked on the under side. The tail, together with the long fur of the body, must supplement to a considerable extent the buoyancy of the patagium. This genus, with its single species, includes the so-called Taguan flying phalanger found in Australia from Queensland to Victoria.

Petaurus (see Fig. 81) has a much broader patagium and there is a naked prepatagium as well. The tail is very large and bushy, but lacks the naked prehensile tip of the preceding form. There are three species of this genus, ranging over New Guinea and part of Australia.

The genus *Acrobates* includes two small species of flying phalangers which have narrow patagia extending from the elbow to the knee along the flank. The long fringing hairs borne by the patagium, together with those on either side of the tail, aid materially in flight. *Acrobates pygmæus* is found in New South Wales, Queensland, and Victoria, while a second species, *A. pulchellus,* is a native of Papua.

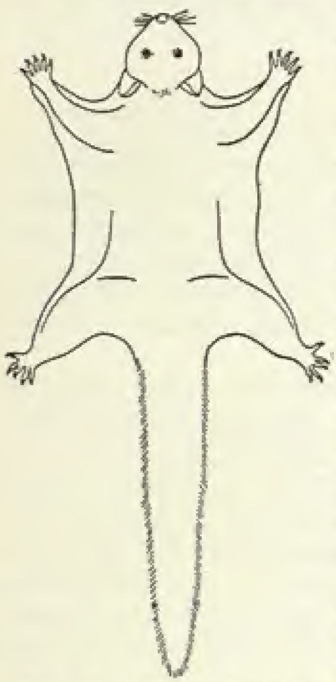


FIG. 81.—Flying phalanger (marsupial), *Petaurus sciureus.* (After Lull.)

Two families of *rodents* contain flying forms: the Anomaluridæ, including the genus *Anomalurus,* and the Sciuridæ, of which three genera, *Pteromys, Sciuropterus,* and *Eupetaurus,* are volant. *Anomalurus* has a well developed patagium extending from wrist to ankle but narrowing in front of the leg from the knee down. As a compensation, however, there is an interfemoral membrane from the heel to slightly beyond the base of the tail. The genus includes six flying species, all found in Africa.

Pteromys has a highly developed patagium extending as far as the digits. There are also prepatagia and an interfemoral membrane, and the tail is large. The genus is found in the wooded districts of tropical southeastern Asia, Japan, and some of the Malasian Islands, and is said to soar through a distance of nearly 80 yards.

Sciuropterus (Fig. 82) has no interfemoral membrane, but has a much better developed tail than *Pteromys* as a compensation. This wide hairy tail is further supplemented by the hairy fringe on the patagium and along the rear of the thighs, and they give collectively a broad supporting area. While members of this genus are smaller than those of *Pteromys,* their geographical range is much greater, as it includes the northern part of the North American and Eurasian continents, and India.

Eupetaurus is of especial interest in that it is not arboreal but rock- and precipice-climbing. It inhabits the high elevations of northwestern Kashmir.

Among the *Insectivora*, *Galeopithecus* (Fig. 70), the sole representative of the suborder Dermoptera, stands alone in its adapta-

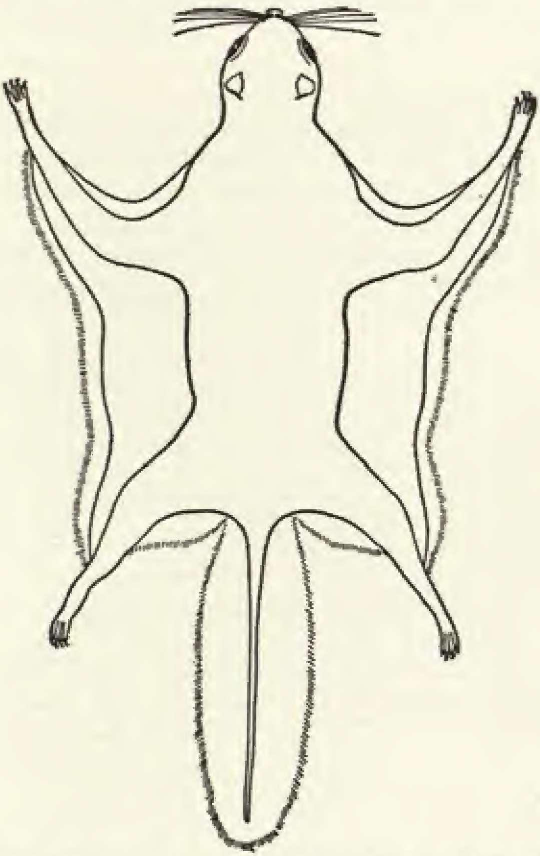


FIG. 82.—Flying squirrel, *Sciuropterus volucella*. (After Lull.)

tion, for it exhibits the highest degree of aviation of any of the Mammalia except the bats, and while not of course ancestral to the latter, it is evidently derived from a common stock and gives a very clear idea of the manner in which the evolution of the bats was accomplished. In this genus the patagium reaches its highest development, as it extends from the rear of the head along the

front of the arm (prepatagium), between the fingers to the base of the claws, between the fore and hind limb, webbing the toes as well as the fingers, and between the hind limbs and the tail (interfemoral membrane), including the entire length of the latter organ as in the insectivorous bats (Microcheiroptera). The musculature and innervation of the patagium resemble those of the bats and differ decidedly from those of all other volant mammals. The hand is much larger than the foot, but the fingers show no trace of elongation. If they did the entire creature would be still more bat-like. As it is, the brain is midway in its development between that of a typical insectivore and that of a bat, and the alimentary canal is also bat-like except for an elongated colon or large intestine, which in the bats and birds is very short.

Galeopithecus is nocturnal, as are most volant mammals, resting suspended, head down, from a branch. Its soaring powers are very

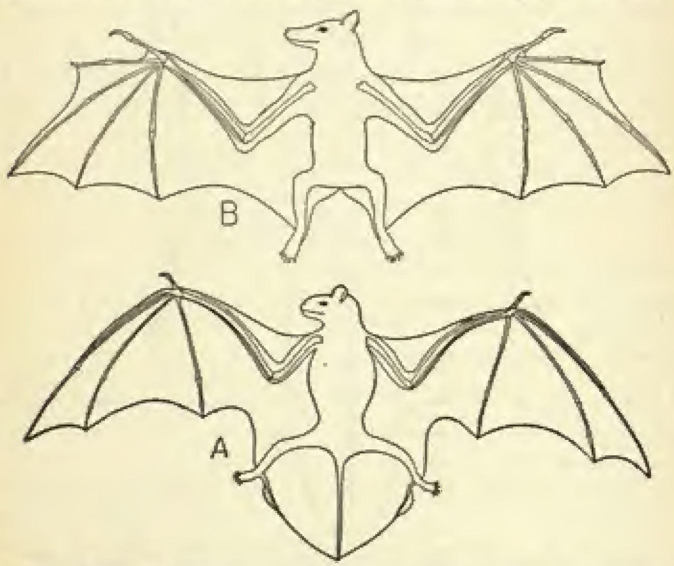


FIG. 83.—Bats. A, insectivorous, *Vespertilio noctula;* B, frugivorous, *Pteropus* sp. (After Lull.)

great, for Wallace tells us of a record of 70 yards with a descent of not more than 35 or 40 feet, or less than one in five. The genus includes two species: *Galeopithecus volans*, from the Malay Peninsula, Sumatra, and Borneo, and *G. philippinensis*, which inhabits the Philippine Islands.

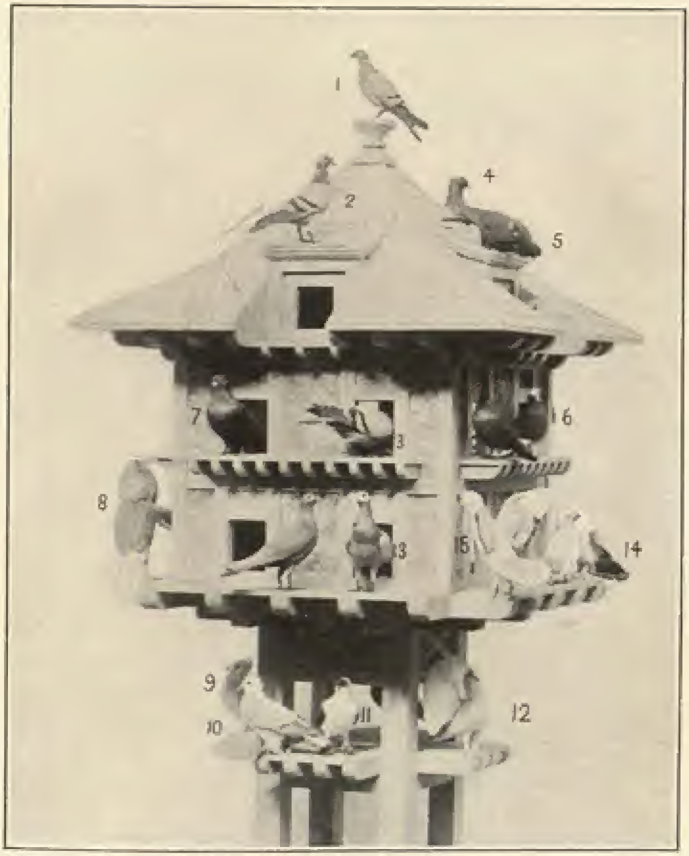
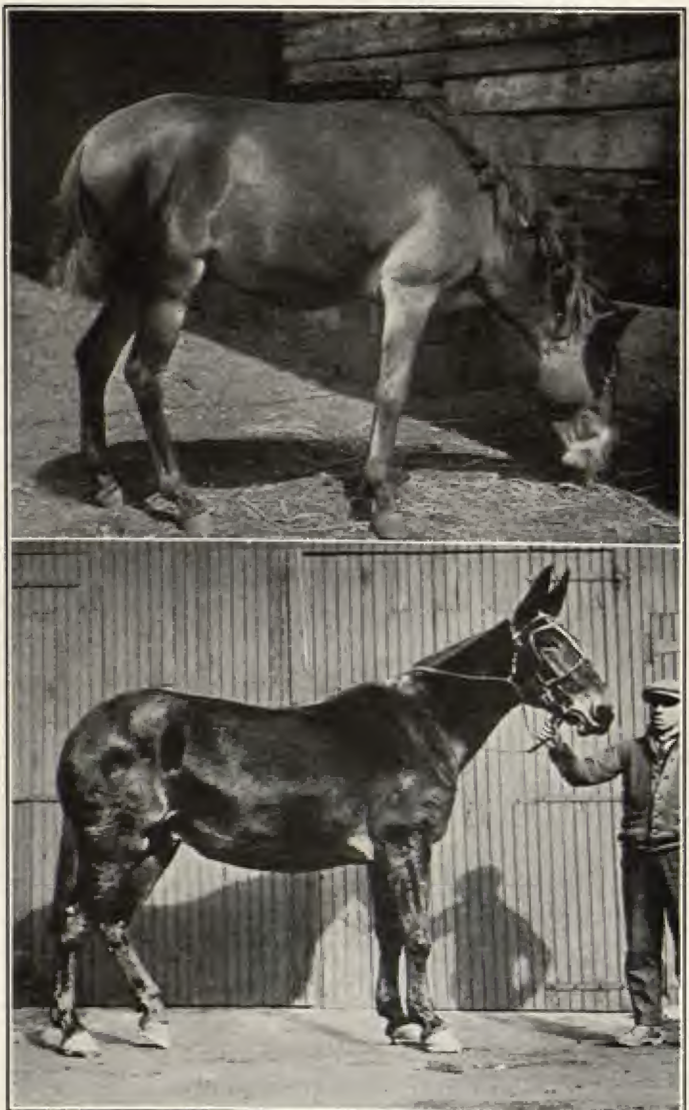


Plate. I.—Domestic varieties of pigeons. 1, wild rock dove, *Columba livia*, ancestral form; 2, homing pigeon; 3, common mongrel; 4, archangel; 5, tumbler; 6, bald-headed tumbler; 7, barb; 8, pouter; 9, Russian trumpeter; 10, fairy swallow; 11, black-winged swallow; 12, fantail; 13, carrier; 14, 15, bluetts; bird between 14 and 15, a tailed turbit. Exhibit in the United States National Museum. (Courtesy of that institution.)



B

A

PLATE II.—Mule (A) and hinny (B). (Courtesy of S. H. Chubb.)

PLATE III.—Skeletons of man, *Homo sapiens*, and rearing horse, *Equus caballus*, to show correspondence of bones, also loss of bones, digits, etc., in the horse. Mounted skeletons in the American Museum of Natural History. (Courtesy of Professor Osborn.)

A

B

PLATE IV.—A, giant cactus, saguaro, *Carnegiea gigantea*, in the desert west of Zapotitlan, Puebla, Mexico. B, cactus forms at head of San Juan Ryan barranca, Puebla, Mexico. (Photographs by Professor Charles Schuchert.)

Plate V.—Beresovka mammoth, *Mammonteus primigenius*, discovered frozen in the soil. Specimen as it now appears in Leningrad.

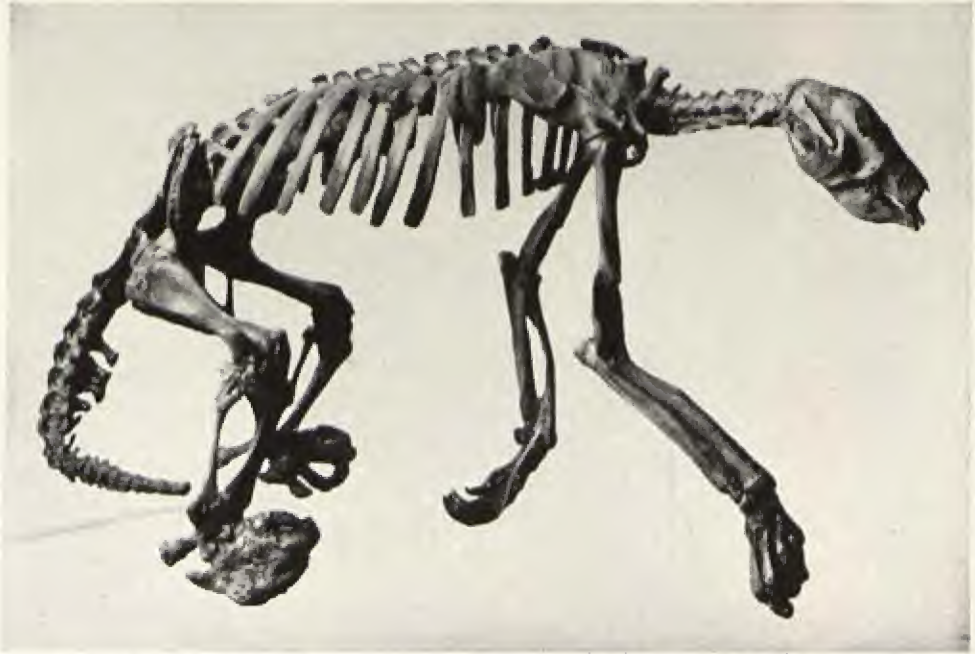
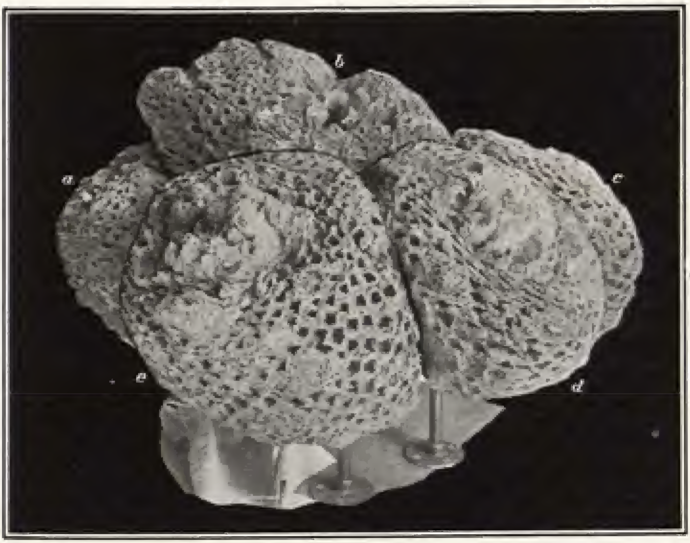
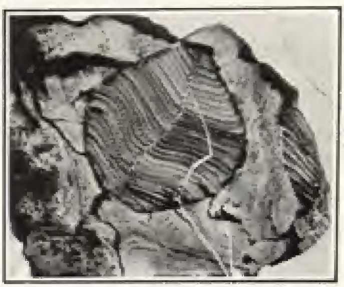


PLATE VI.—Ground sloth, *Nothrotherium shastense*, Pleistocene, New Mexico. Skeleton with portions of hide, claws, etc., adhering. Specimen in the Yale Peabody Museum.



A



B

PLATE VII.—A, cycad trunk, *Cycadeoidea superba*, from the Lower Cretaceous (Lakota) of the Black Hills, South Dakota. B, section of a fossil cycad, *C. ingens*, showing molecular structure, histometabasis; a young undeveloped frond, showing the vascular bundles. Specimens in the Yale University Museum.

PLATE VIII.—Pompeian dog. Plaster cast from a natural mould.

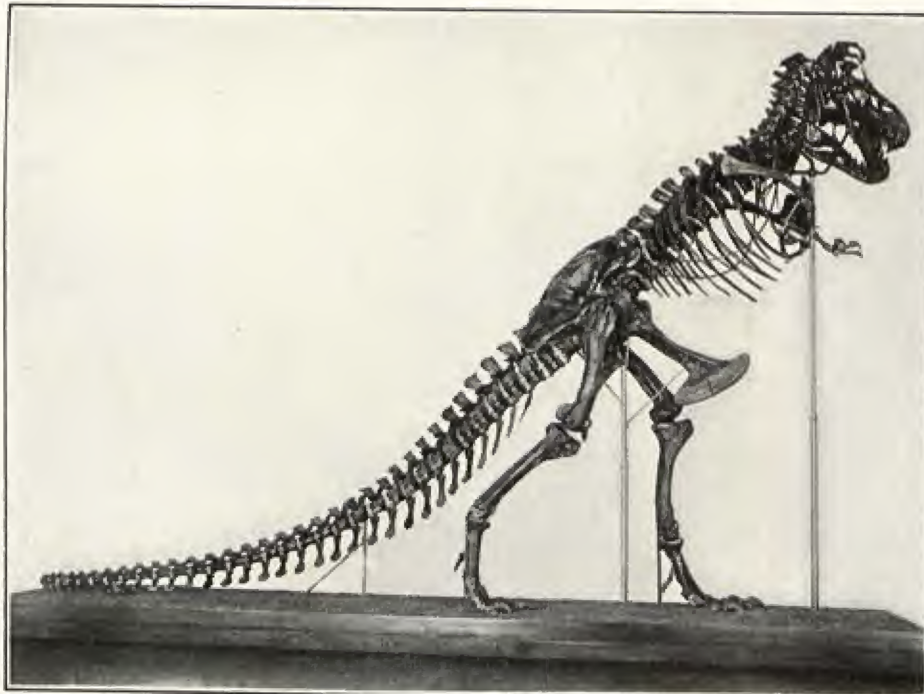


PLATE IX.—Skeleton of the greatest carnivorous dinosaur, *Tyrannosaurus rex*, mounted in the American Museum of Natural History. (Courtesy of Professor Osborn.)

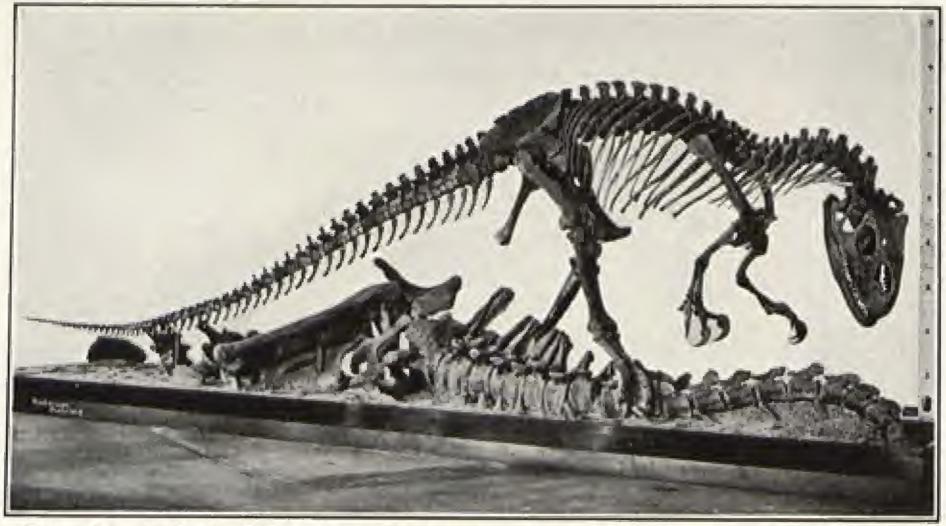


PLATE X.—Skeleton of the carnivorous dinosaur, *Allosaurus fragilis*, mounted in the American Museum of Natural History. The creature is represented as preying upon the carcass of one of the contemporary sauropods. (Courtesy of Professor Osborn.)

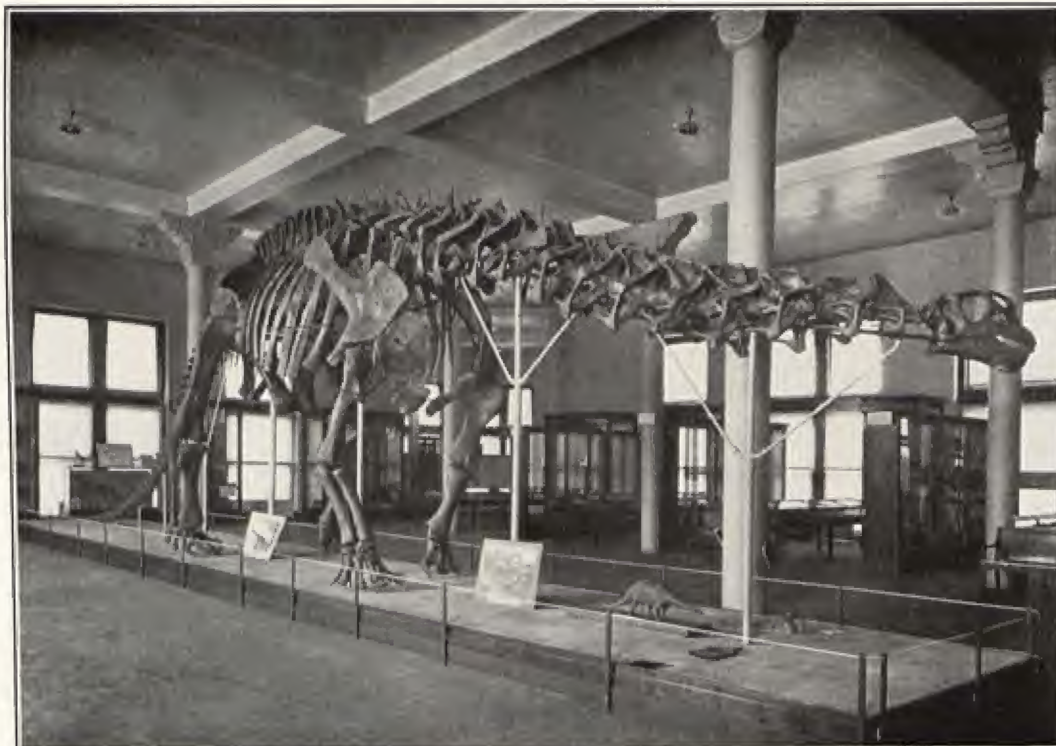


Plate XI.—Skeleton of the sauropod dinosaur, *Brontosaurus excelsus*, mounted in the American Museum of Natural History. (Courtesy of Professor Osborn.)

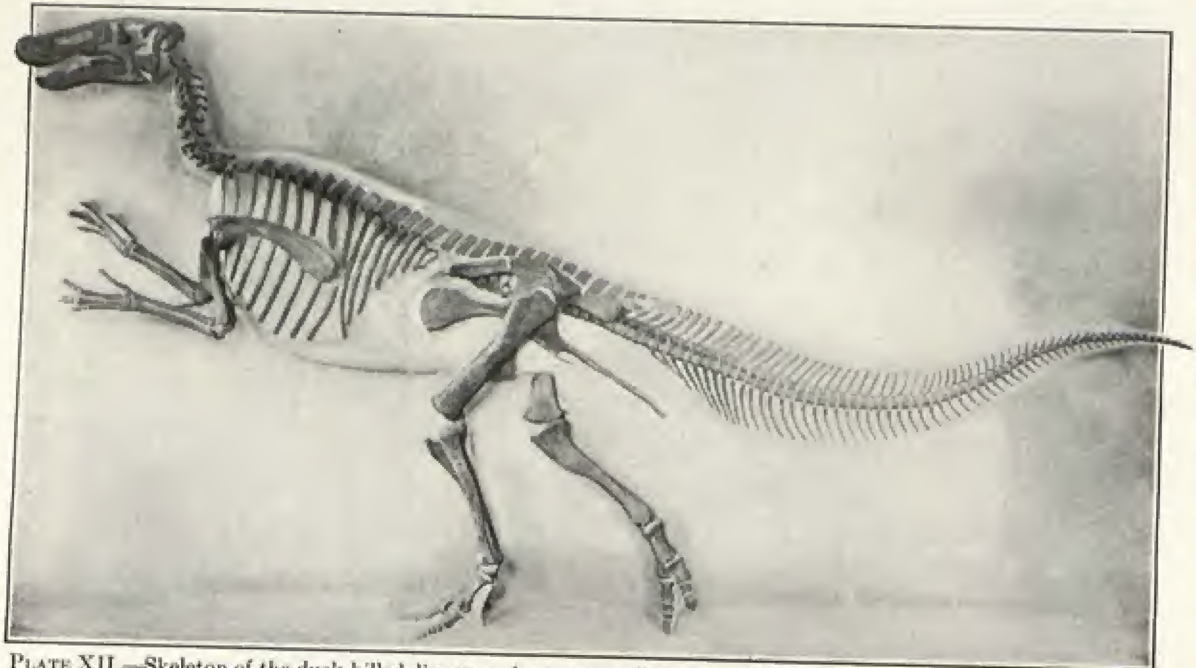


PLATE XII.—Skeleton of the duck-billed dinosaur, *Anatosaurus (Claosaurus) annectens*, mounted in the Yale Peabody Museum. The first actual dinosaur skeleton mounted in the United States.

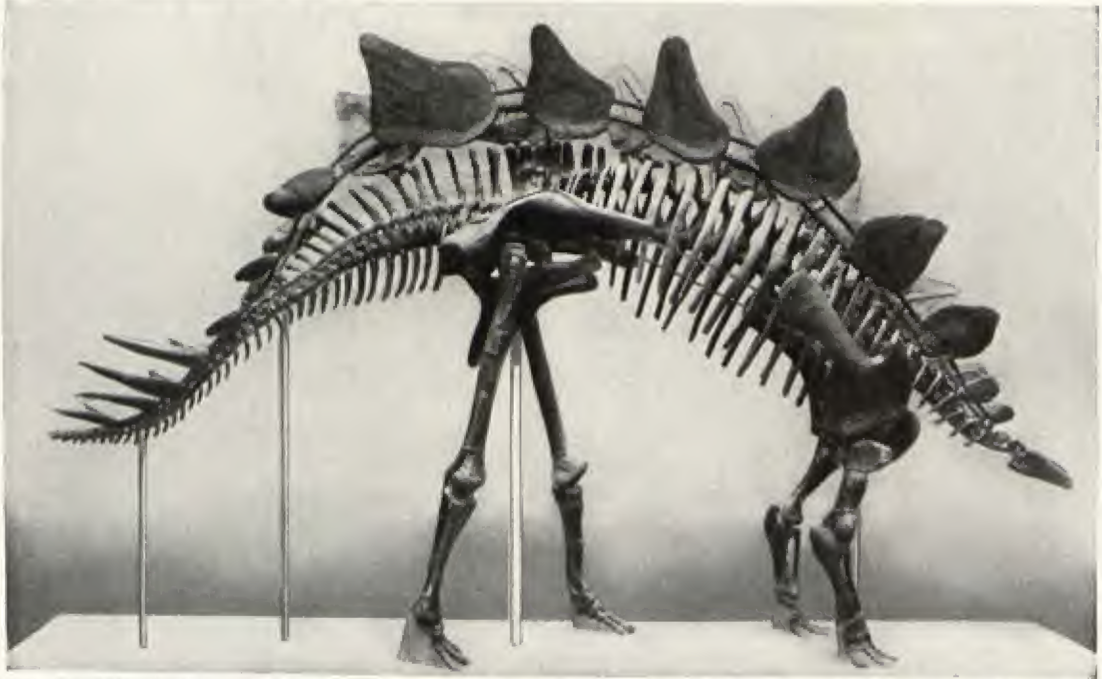


PLATE XIII.—Skeleton of the armored dinosaur, *Stegosaurus ungulatus*, Upper Jurassic (Morrison) of Wyoming, mounted in the Yale Peabody Museum.

PLATE XIV.—The earliest known bird, *Archæornis*, from the Upper Jurassic of Bavaria. (Restoration by Heilmann.)

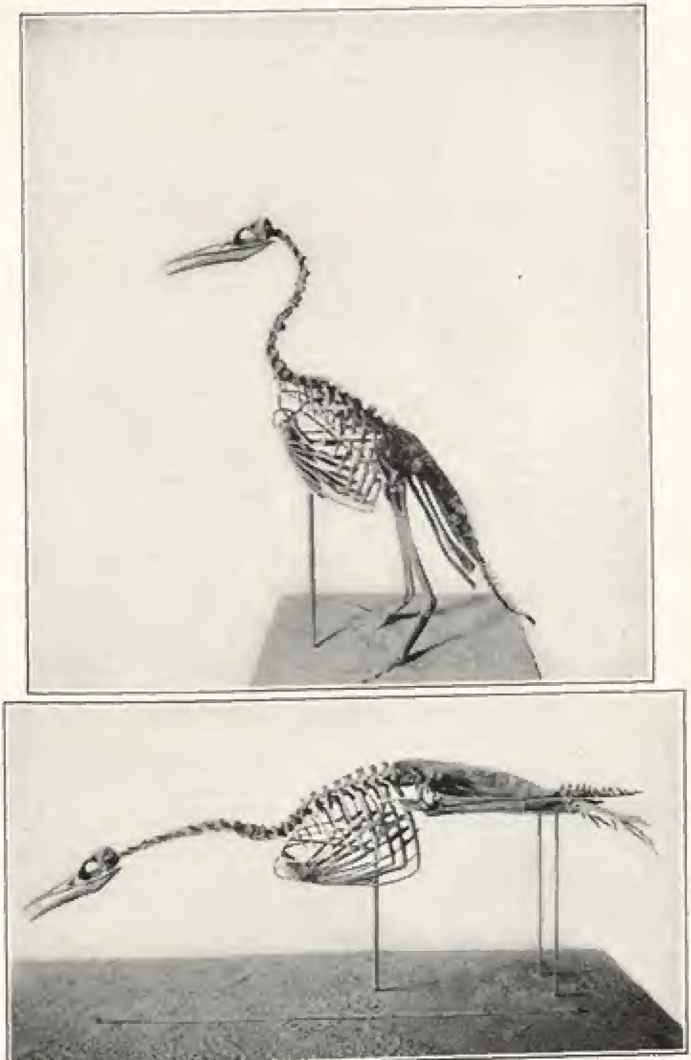


PLATE XV.—Skeletons of *Hesperornis*, a toothed diving bird from the Cretaceous (Niobrara) of Kansas. Standing specimen, *H. regalis*; swimming, *H. crassipes*. Mounted skeletons in the Yale University Museum.

Plate XVI.—Tooth of a carnivorous dinosaur, *Allosaurus!*, and the entire jaw of a contemporary mammal, *Dicrocynodon*, found in association in the same quarry. Jurassic of Como Bluff, Wyoming. Both two-thirds natural size. Specimens in the Yale University Museum.

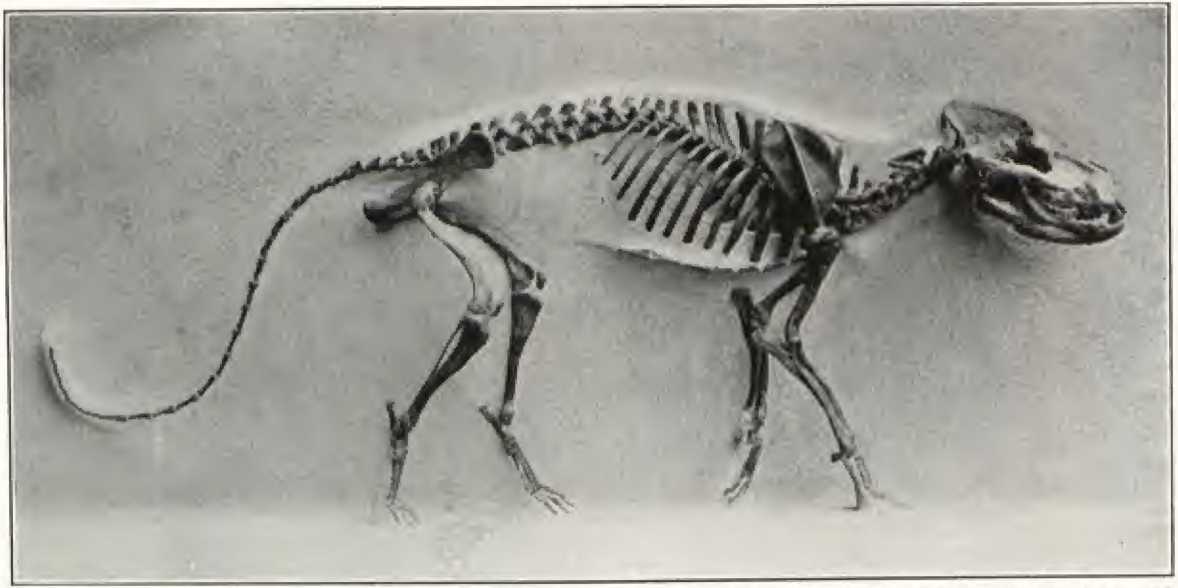


PLATE XVII.—Skeleton of the dog-like creodont, *Dromocyon vorax*, Middle Eocene, (Bridger) Wyoming. Mounted skeleton in the Yale University Museum.

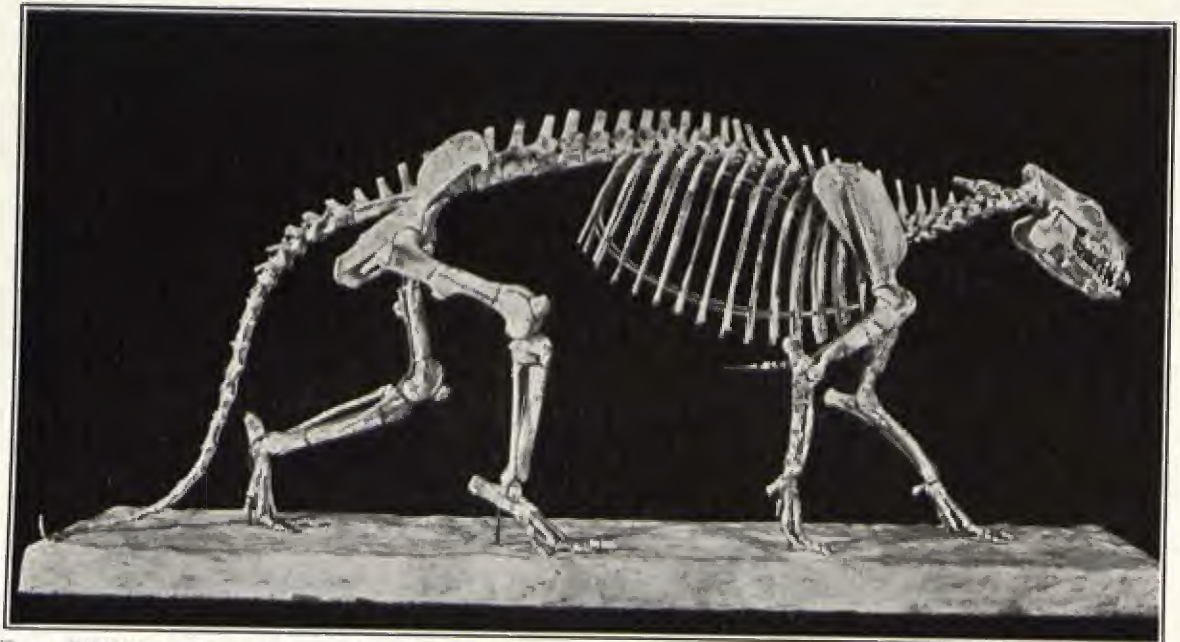


PLATE XVIII.—Skeleton of the condylarth, *Phenacodus resartus*, Lower Eocene (Wasatch), Wyoming and New Mexico. Mounted skeleton in the American Museum of Natural History. (Courtesy of Professor Osborn.)

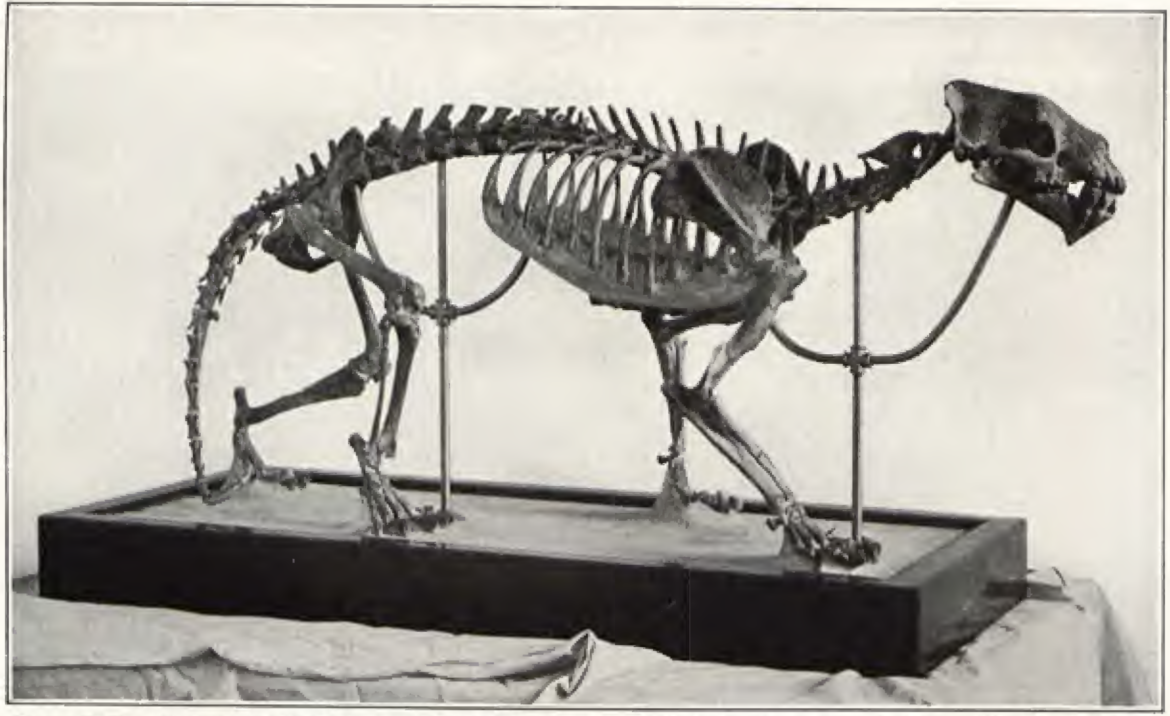


PLATE XIX.—Skeleton of *Hoplophoneus*, Middle Oligocene, South Dakota, a forerunner of the great Pleistocene sabertooth. Mounted skeleton in the American Museum of Natural History. (Courtesy of Professor Osborn.)

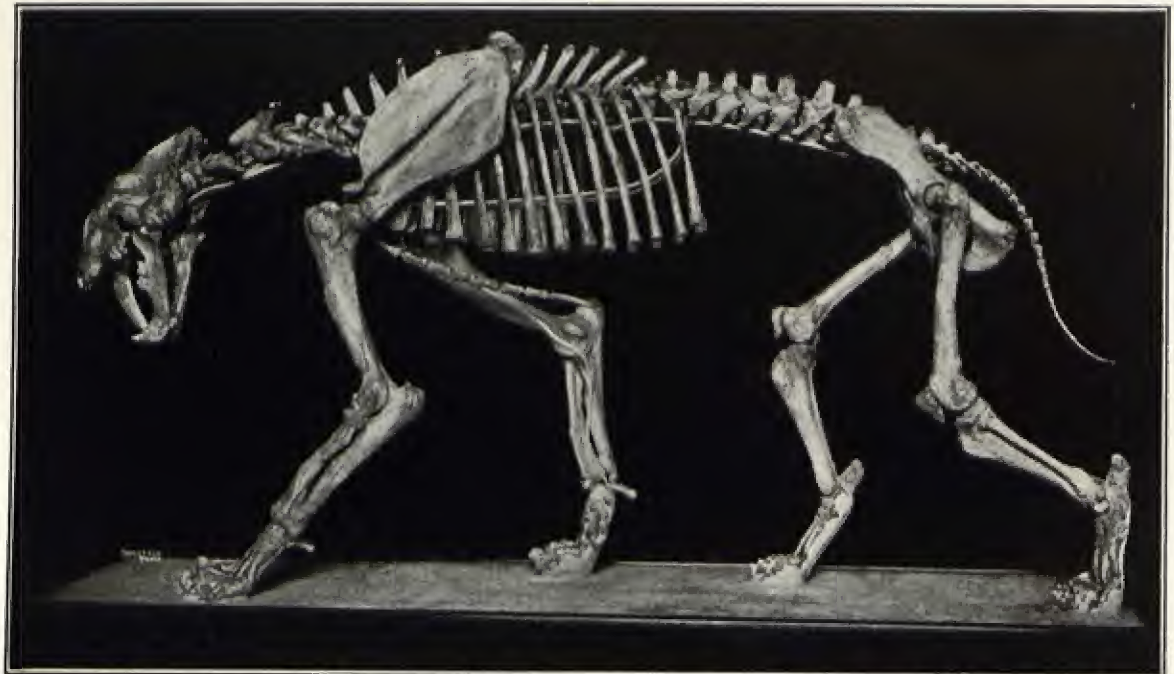


PLATE XX.—Skeleton of the great saber-tooth, *Smilodon neogæus*, Pleistocene, South America. Note the loss of one of the sabers. Mounted skeleton in the American Museum of Natural History. (Courtesy of Professor Osborn.)

Plate XXI.—African elephant, "Jumbo," *Loxodonta africana*, from a photograph taken in the London Zoölogical Garden.

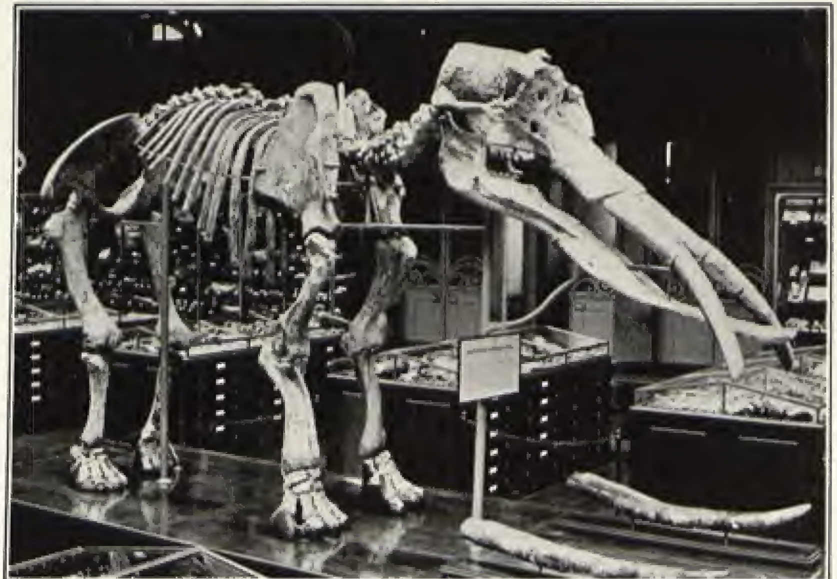


Plate XXII.—Skeleton of the four-tusked mastodon, *Trilophodon* (= *Tetrabelodon*) *angustidens*, Lower Miocene, Africa and Europe. Mounted skeleton in the Jardin des Plantes, Paris. (Courtesy of Professor Boule.)

A

B

PLATE XXIII.—African (A, young individual) and Asiatic (B) elephants. (Photographs from the New York Zoölogical Society.)

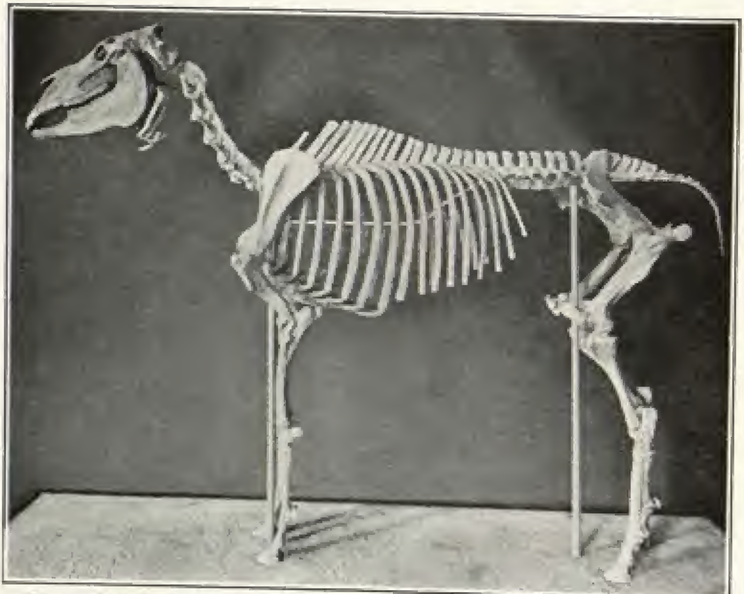


PLATE XXIV.—Skeleton of the one-toed horse, *Equus scotti*, the last of the American evolutionary line, Pleistocene, Texas. Mounted skeleton in the Yale Peabody Museum.

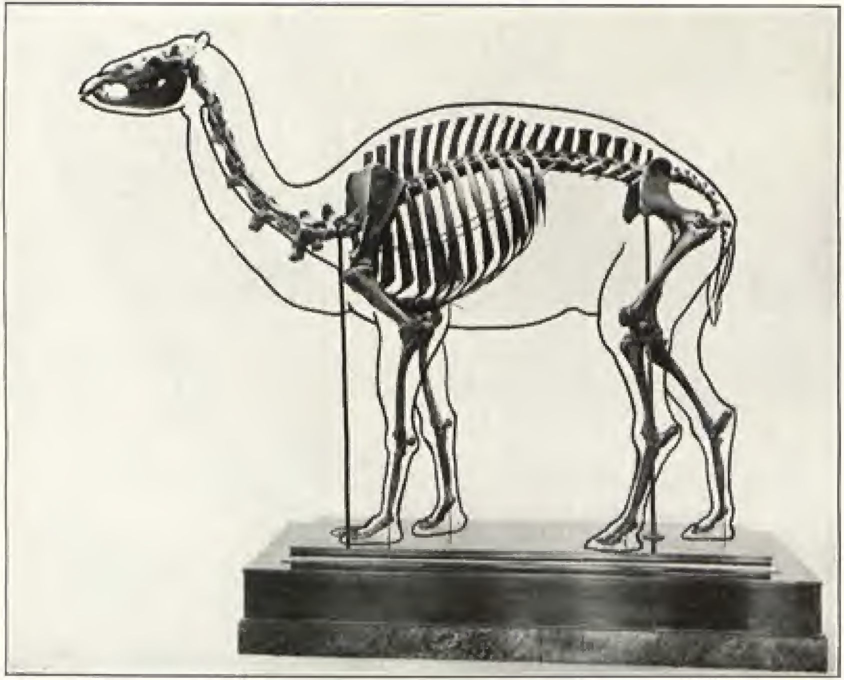


Plate XXV.—Skeleton of *Camelops hesternus* from the Pleistocene (asphalt) of the Rancho la Brea, California. (Courtesy of the Los Angeles Museum.)

Plate XXVI.—Gelada Baboon, *Theropithecus gelada*, Southern Abyssinia "An insanely animated caricature of a lion"—Ditmars. (Photograph from the New York Zoölogical Society.)

PLATE XXVII.—Gibbon, *Hylobates lar*, southeastern Asia. (Photograph from the New York Zoölogical Society.)

Plate XXVIII.—Orang-utan, *Simia satyrus*, Sumatra and Borneo. (Photograph from the New York Zoölogical Society.)

PLATE XXIX.—Chimpanzee, *Pan pygmæus*, western and central equatorial Africa. (Photograph from the New York Zoölogical Society.)

PLATE XXX.—Gorilla, *Gorilla gorilla*. Mounted specimen in the American Museum of Natural History.

A

B

C

D

PLATE XXXI.—Restoration of prehistoric men, after models by J. H. McGregor. A, *Pithecanthropus erectus*, the Ape-man of Java; B, *Eoanthropus dawsoni*, the Piltdown man; C, *Homo neanderthalensis*, the Neanderthal man; D, *Homo sapiens*, the Crô-magnon man. (Courtesy of Professor McGregor.)

"Nature knows very well that the attack will come and so she provides her plants with various different defenses. The most common weapon which she gives them is the spine or thorn. Almost everything that grows has it and its different forms are many. They are all of them sharp as a needle and some of them have saw edges that rip anything with which they come in contact. The grasses, and those plants akin to them like the yucca and the maguey, are often both saw-edged and spine-pointed. All cacti have thorns, some straight, some barbed like a harpoon, some curved like a hook. There are chollas that have a sheath covering the thorn—a scabbard to the sword—and when anything pushes against it the sheath is left sticking in the wound. The different forms of the bisnaga are little more than vegetable porcupines. They bristle with quills or have hook-shaped thorns that catch and hold the intruder. The sahuaro has not so many spines, but they are so arranged that you can hardly strike the cylinder without striking the thorns."

Of the *chemical characteristics* which serve the plants for defense, the first to assail one's senses is the strong aromatic character of desert vegetation. Both odors and tastes are very pronounced and may prevent the plant from being eaten just as the spinescence does. A notable instance is the very characteristic sage brush of the western plains which no mammal will eat except the jack-rabbit and no bird except the sage hen, and the flesh of each is so thoroughly impregnated by the sage that no human being will eat either of them if any other food is available. Neither the rabbit nor the chicken will eat the sage during their first summer and then the flesh of each is most palatable. The greasewood is another disagreeable tasting plant with sticky varnished leaves which nothing will eat, and the sangre-de-dragon has a blood-red sap which is so powerfully astringent that the Indians use it to cauterize bullet wounds.

Thus, aside from being disagreeable to the taste and smell, many plants are actually poisonous, some cathartic, others emetic in their effects, while one, the loco weed (*Astragalus hornii*) produces, aside from bodily alterations, symptoms in domestic stock comparable to insanity, hence the term "locoed" as applied to one mentally deranged (Span. *loco*, insane). Horses and cattle do not touch the loco plant for the first time voluntarily, but as with many other forms of narcotic, the habit accidentally acquired is almost impossible to break.

It would seem again as though these chemical characteristics were of great defensive value, and doubtless they are; but whether that is a sufficient *cause* for their being what they are, or whether it is due to desert conditions regardless of the presence of devouring animals is not quite so clear. The aromatic character is so prevalent among desert plants, whether used as food or not, that it leads one to question whether or no defense is a prime cause in the evolution of this characteristic. The gazelle, one of the most admirably adapted of desert animals, is confined to tufts of wiry grass and a few dwarf and strongly scented aromatic herbs for food. That these agree with it is attested by the fact that the number of gazelles in some parts of the Arabian desert is extraordinary and vast herds have occasionally been met with.

Another conception of the origin of the chemical characteristics of desert plants is that they are merely a response to aridity. It is well known that saline lakes are characteristic of arid climates, and to the geologist the presence of beds of salt or gypsum or other alkaline substances is indicative of desert conditions in bygone times. These salt lakes are thus described by Pirsson: Part of the river's burden "consists of various salts in solution and such salts are carried by all streams, even if, in a given volume, the water appears so fresh that they can only be detected by chemical means. In ordinary rivers these salts are discharged into the sea, but in interior drainages [*i. e.* such as end in evaporation] since they cannot be dissipated by evaporation like the water, they must constantly accumulate at the point where the drainage ends.

"If the river ends by dwindling, its lower part finishes in a stretch covered with salt deposits, sometimes in wet seasons converted into a salt marsh or shallow salt lake, and known as a salina. Examples of these are found in the Tarim River which ends in the desert of Gobi in central Asia, in the Desaguedero River which carries the drainage from Lake Titicaca in Bolivia, and in many other places. But if the end of the drainage system is a lake the latter is bound in time to become salt through the concentration of these substances, and such salt lakes are features of arid or desert regions in all the continents." Examples are the Dead Sea in Palestine, Lakes Baikal and Balkash and the Aral Sea in Siberia, and in North America the Great Salt Lake in Utah, Pyramid Lake and others in Nevada, and Mono Lake in California.

The idea has been expressed that the chemicals which impregnate

desert plants may have an analogous source—water more or less laden with these salts is drawn from below by the roots and, being dissipated ultimately into the air by evaporation, leaves the substances behind as a residue which may in turn be elaborated by the plant into the characteristic aromatic or saline chemical. If this be true, it would account for these characteristics without invoking the need of defense, but one would expect to find, as in thorny growths, a lessening of the chemical attributes as one passes from the arid to a more humid region.

Animals.—Against physical conditions the animal must find means of protection and the first of these conditions is that of the *temperature extremes* so characteristic of arid climates, for while moisture in the atmosphere is transparent to light, it is opaque to heat. Hence where the air is laden with water—either diffused or in the form of clouds—not only does less solar heat penetrate to the ground during the day but less is radiated into space during the night. Therefore some of the highest temperatures recorded are not under the equator where it is humid but in northern Africa and in Asia Minor where dryness prevails. Solimos in his *Desert Life* informs us that the "'sand temperature one day marked 146° Fahr.—temperatures of 170° Fahr. were also found near Jaffa, and Duveyrier found the Sahara one day over 182° Fahrenheit.' But these would probably be sun temperatures. On other occasions he tells us 'Matches were lit by touching the sand with them. Blankets drawn over one another or even slightly shifted, blazed up like sheet lightning. The heat was 109° Fahr. among clothes in a trunk, and 111° Fahr. in the wind: combs, vulcanite, bone or horn, became brittle and useless.'" Again, the German traveler, Doctor Barth, after describing the great heat of the desert in southern Tripoli, mentioned that the guide of the Arab caravan begged him to beware of the cold during the night, which he represented as very intense, and it is a fact well known to all travelers that though the heat in the Sahara is often very extreme by day, the nights are uniformly cold, when the hot wind does not blow (Madden).

Thus the desert animal, unprovided as he is with additional garments, must seek out "the shadow of a great rock in a weary land" by day or if none be available he must burrow and thus escape the extremes of heat and cold, which might prove fatal.

Defense against the ubiquitous *sand* is a prime need, for sand assails three vulnerable portions of the creature's economy—the eyes,

ears and nostrils. Desert reptiles, among other marked adaptations, have these vital organs protected as follows: "In the digging species the nostrils are directed upwards instead of forwards; in most of the snakes they are protected by complicated valves, or they are reduced to small pinholes. The eyes of *Typhlops* [a burrowing desert snake] are overhung by the head-shields. In *Agama* and *Phrynocephalus* [lizards] the margins of the lids are broadened into plates and are furnished with peculiar scales. In *Teratoscincus* the upper lid is enlarged. The lizard *Mabuia* has the lower lid enlarged, with a transparent window in it, so that the eye can be closed without impeding sight, an arrangement carried to the extreme in *Ablepharus* [whose lower eyelid is transformed into a transparent cover, which is fused with the rim of the reduced upper lid, exactly as in the Lacertine genus *Ophiops*]. The ear-opening is either small, or protected by fringes of scales, or it is abolished, *e. g.*, in *Phrynocephalus*" (Gadow).

The camel again shows its desert adaptation in the large eyes, necessary for an animal which relies so much upon vision for security, but they are guarded by long, abundant eyelashes, and the level carriage of the head, seen also in the desert ostrich, brings the eyes as far as possible above the sand—nine feet in the camel, seven in the bird. This is also a response to the reflected heat of the blistering sand and rocks. The camel's nostrils are capable of being closed like eyelids, and the apertures of the ears are protected by hair.

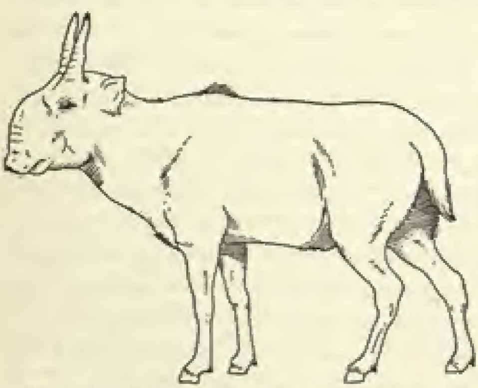


FIG. 90.—Saiga antelope, *Saiga tartarica*. (After Geikie.)

The saiga antelope (*Saiga tartarica*, Fig. 90) is a typical desert form found fossil (Pleistocene) in England but now confined to eastern Europe and western Asia. This peculiar beast has a large and much inflated nose, the two nostrils being widely separated and very short and the narial apertures of the skull placed very far back like those of certain extinct types (such as the horse *Hip-*

pidion, see Fig. 232). This whole device is for the exclusion of sand from the breathing apparatus while the animal is grazing.

Coloration is the first and perhaps the most conspicuous of the adaptations which furnish protection *against other animals*. No greens are seen among desert creatures, but they are generally sympathetically tinted—gray, brown, or red, harmonizing with the color of the sand or rock. Sometimes the same species will show double color adaptation to suit local conditions. Thus the gazelle, Madden tells us, "furnishes a conspicuous and very beautiful example, so closely do their coats resemble the general coloring of the landscape [white on sand, dark grey on volcanic rock] that in the distance, and when at rest, it is scarcely possible to distinguish them from the surrounding sand and stones." Van Dyke says of the coyote: "He is cunning enough to know . . . that you cannot see him on a desert background as long as he does not move; so he sits still at times for many minutes, watching you from some little knoll. As long as he is motionless your eyes pass over him as a patch of sand or a weathered rock."

Warning coloration is often seen in the desert, and as a rule it is not merely the *mimicry* of a dangerous form but the actual livery of one which should not be molested if the assailant would escape unscathed, for venomous spiders and insects and reptiles are common. Here for instance is found the conspicuous yellow and black Gila monster, the only lizard with poison fangs; and conspicuously marked wasps, while not, perhaps, actually dangerous to humanity, are to the creatures with which they compete.

Hard surface and spinescence are as characteristic of desert insects and some reptiles as they are of desert plants. The moloch (Fig. 91) with the thirsty skin which has been described is covered with thorn-like scales, and the horned toad is a conspicuous American instance of spinescence. Here, as with the plants, the spinescence loses its intensity of development as one passes into the more humid regions, for while in the horned toads of the Southwest the horns at the back of the head are long and prominent, in those of Wyoming and Nebraska they are much less conspicuous.

Venom has already been referred to as a desert attribute. Van Dyke again sums the matter up most admirably, although he speaks of more than the reptiles with which he introduces his remark. He says of them:

"They are given the most deadly weapon of defense of all—

poison. Almost all of the reptiles have poison about them in fang or sting. We are accustomed to label them 'poisonous' or 'not poisonous,' as they kill or do not kill a human being; but that is not the proper criterion by which to judge. The bite of the trap-door spider will not seriously affect a man, but it will kill a lizard in a few minutes. In proportion to his size the common red ant of the desert is more poisonous than the rattlesnake. It is reiterated with much positiveness that a swarm of these ants have been known to kill men. There is, however, only one reptile on the desert that humanity need greatly fear on account of his poison and that is the rattlesnake. . . . The rattle is indescribable, but a person will know it the first time he hears it. It is something between a buzz and a burr, and can cause a cold perspiration in a minute fraction

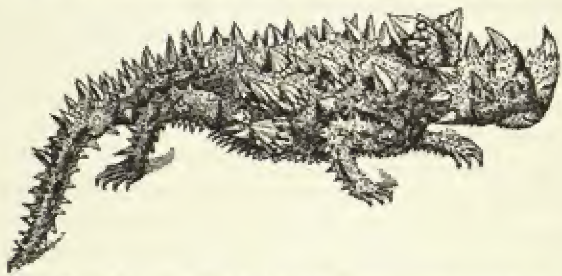


FIG. 91.—Spiny lizard. *Moloch horridus.* (After Gadow.)

of time. . . . Every animal on the desert knows just how venomous is that poison. Even your dog knows it by instinct. He may shake and kill garter-snakes, but he will not touch the rattlesnake.

"All of the spider family are poisonous and you can find almost every one of them on the desert. The most sharp-witted of the family is the trap-door spider—the name coming from the door which he hinges and fastens over the entrance of his hole in the ground. The tarantula is simply an overgrown spider, very heavy in weight, and inclined to be slow and stupid in action. He is a ferocious-looking wretch and has a ferocious bite. It makes an ugly wound and is deadly enough to small animals. The scorpion has the reputation of being very venomous; but his sting on the hand amounts to little more than that of an ordinary wasp. Nor is the long-bodied, many-legged, rather graceful centipede so great a poison-carrier as has been alleged. They are all of them poisonous, but in varying degrees."

The skunk of the Southwest is greatly feared by the natives as its bite is supposed to produce skunk hydrophobia. In reality, however, it is blood-poisoning that results from the bite, for the skunk feeds on carrion and its teeth, defiled with the remains of its last meal, inject some of the putrescent material into the wound caused by its bite. It is probable that in many of the desert creatures the dangerous reputation is altogether undeserved. The native cook of a certain Yale expedition to the Southwest had the entire personnel in terror of its life from the only arachnid which does *not* possess poison fangs!

Speed, as we have seen, is a characteristic of the dwellers in arid climates, for they have to travel far and wide for food and drink or to pursue or evade pursuit as the case may be. There is so little cover and the creature in motion can be seen so far that speed becomes a prime requisite in many unrelated types. Many of the lizards are so swift that the eye loses sight of them as they dart from rock to rock, and some run on the hind limbs for greater rapidity. Some birds, as the ostrich or the road runner or chaparral cock of the Southwest, are noted for their speed. The gazelle, wild ass, and camel again are great travelers, while a desert jackrabbit finds his match only in a greyhound—an ordinary wolf or coyote will not attempt to chase him, for they realize the hopelessness of it. The western antelope, *Antilocapra*, even with a limb shot from under him, has been known to outdistance a horse, and with all four limbs the run is so easy and so deceptive that a gunner almost always underestimates the speed and places his bullet behind the fleeting game. Even the domestic cattle on the western ranges have an ease and speed in running which is a revelation to an easterner.

This speed shows itself in the slender form, long limbs, and often in the sand-adapted feet of the desert wayfarer. Those of the camel, with the broad, yielding pad and secondary retrogression from unguligrade to digitigrade, are splendidly fitted to the yielding sands. Of the desert lizards, *Eremias* has very large crural (shank) shields; *Scapteira* has the digits broadened out into shovels; others, *e. g.*, *Phrynocephalus* and *Teratoscincus*, have long lateral fringes on the digits, a very rare arrangement among geckoes, occurring elsewhere among them only in *Ptenopus* and *Stenodactylus*, which are likewise inhabitants of the desert (Gadow).

The **senses** of sight, hearing, and smell are highly developed as contrasted with those in forest-dwelling forms, for instance, whose vision is notoriously dull even though hearing and smell may be acute enough. Sometimes about all one can see of a desert rabbit, frozen into immobility through fright, are the large, clear, watchful eyes which never seem to close.

Intelligence is also a desert desideratum, especially among defenseless, that is, non-venomous forms, for the Gila monster seems to be superlatively stupid while the others must match their wits as well as length of limb if they would survive.

As we shall see in later chapters, the wide-spread desert and semi-desert conditions which have occurred from time to time in the geologic past have been of prime importance as evolutionary stimuli, and have given rise to some of the most momentous changes in organic life.

Colonial Life

The plant life of the desert is not evenly spread as in humid regions, but is in scattered, discontinuous colonies with long stretches of verdureless sand in between. Moreover, these communities are composed of several species, not only of one, for while the interspecific struggle in the desert is intense, that against a relentless physical environment is more so, so that coöperation becomes of greater moment than exclusive self-advancement. McGee says:

"The various plants of the [Seri] district, including those of the distinctive types, are communal or commensal, both among themselves and with animals, to a remarkable degree; for their common strife against the hard physical environment has forced them into coöperation for mutual support. The tufts or clusters in which the vegetation is arranged express the solidarity of life in the province; commonly each cluster is a vital colony, made up of plants of various genera and orders; and forming a home for animal life also of different genera and orders; and, although measurably inimical, these various organisms are so far interdependent that none could survive without the coöperation of the others."

The **origin of the communities** has been well summed up by Van Dyke: "Mesquite springs up on the plain, birds nest in the branches, drop seeds of cacti some of which like vines cannot stand alone, armature of cacti and mesquite combine for protection.

Windblown grass seeds lodge about the roots and grasses grow and seed beneath the shelter of the branches. Small mammals seek some protection and dig holes among the roots, making channels for rain and fertilizing the spot with rejectamenta. Annual and semi-annual plants take root in the sheltered and fertilized soil beneath the cacti and mesquite and in season the place becomes a miniature garden of foliage and bloomage. Then come certain ants for seeds, flies and wasps for nectar, and birds nest in the branches. Such communities dot the vast plains, intermediate stretches are practically lifeless."

Origin of Desert Life

The desert floras are all local adaptations of migrants from more humid regions, except the cacti and torotes, which seem to be the products of aridity, since neither is represented in the flora of humid regions. Of the animals, all are forms whose range is greater than the desert limitations; nevertheless some of them, like the camels, are so perfect and ancient an adaptation to desert life that when, during the Miocene, we find the first indications of retrogression of the feet (see Chapter XXXVII) we can safely infer the beginning of aridity if we had no other evidence. A few animals are desert-adapted, others may be merely temporary migrants desertward, returning to more salubrious places from time to time. Many of these latter creatures go to the desert during its periods of fertility and the numbers of species which have been noticed as occasional visitors is very large; but as the waters dry up and the vegetation begins to wither, these take their departure in common with the desert nomads and their flocks; of whom a regular exodus then begins (Madden).

Summary

The modifications of desert animals and plants, while in many instances wonderful in their detail and of the utmost importance in the struggle for existence, are largely, as in the cave, the result of response to unfavorable conditions—not of course to darkness, so that degeneracy other than the loss of leaves rarely occurs, but to the nature of the soil, to extremes of temperature, and to thirst and hunger. The fact that so many of the seeming desert characteristics lose their extreme of development as aridity diminishes is evidence for this. The plant adjusts itself to, the animal

flies from, and the man modifies the desert conditions—for a time—but all the intelligence and engineering science he has brought into the combat only prevail for a while, as the ruins of ancient cities in central and western Asia attest. For man's conquest of the desert is like his so-called command of the sea—which tolerates him and his mightiest creations during her more complacent moods, then storm and ice and fog combine and the proud fabric which he boastfully calls *Titanic* perishes. Man for a brief space may dominate the desert, but sooner or later the desert will claim its own.

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SECTION 3. PALEONTOLOGY

CHAPTER XXV

FOSSILS: THEIR NATURE AND INTERPRETATION

The term *fossil* is thus defined in the *Encyclopædia Britannica:* "(L. *fossilis*, from *fodere*, to dig up.) Since the time of Lamarck reserved to include only the remains or traces of plants and animals, preserved in any natural formation whether hard rock or superficial deposit, not only petrified structures of organisms but whatever was directly connected with or produced by these organisms."

In general, the idea of antiquity is associated with our conception of a fossil, as for instance in that of Barnard, whose definition reads: "The remains of animals and plants which have existed on the earth in epochs anterior to the present and which are buried in the earth." By Geikie, however, the idea of antiquity is not necessarily included, for his notion of the term embraces "the bones of a sheep buried under gravel and silt by a modern flood," as well as "the obscure crystalline trace of a coral in ancient masses of limestone." The idea of burial, however, by some natural agency, either by water- or wind-borne sediments or by being engulfed in bog or quicksand, is always implied.

Nature of Fossils

To many the term fossil implies a petrifaction—literally a turning to stone—and while in many instances the gradual addition to or replacement of the organic material by some mineral substance has occurred, that is not always the case, so the student has come to recognize several sorts of fossils and to group them under the following heads.

Actual Preservation Intact.—In nature's cold storage warehouse, notably in the arctic tundras of Siberia, frozen either in the paleocrystic ice or in the soil itself, are found animal remains with more or less of the original substance intact. How many such remains have been found is doubtless unrecorded, as they were in more than one instance swept away by the waters as the ice broke up, or were devoured by dogs and wolves, possibly by the natives

themselves though the latter regard such objects with superstitious terror. Of the two most remarkable of these specimens the first was found frozen in clear ice in the Lena delta in 1799 and secured in 1806, and the skeleton, now mounted in the museum of the Leningrad Academy, has remains of the hide still adhering to the skull and feet. A century later, in 1901, the second specimen (see Pl. V) was found at Beresovka, Siberia, 800 miles west of Bering Strait and 60 miles north of the Arctic Circle. This creature evidently slipped into a natural pitfall of some sort, possibly an ice crevasse covered with soil and vegetation. A fractured hip and fore limb, a great mass of clotted blood in the chest, and unswallowed food between the clenched teeth all point to the violence and suddenness of its passing. Almost all of the animal was preserved, though the hair of the back had disappeared and the trunk had been eaten off by dogs before the specimen was discovered. The mounted skin in the posture in which it was found, with the skeleton in walking attitude beside it, together with various soft parts preserved in spirits, are also to be seen in the Leningrad Museum.

Remains of mammoths have likewise been found in Alaska, but thus far no even approximately complete specimens have been secured.

The woolly rhinoceros (*Rhinoceros tichorhinus*) has also been found frozen in the ice, but the greater part of the carcass was swept away by the water and irrevocably lost. Skulls, however, have often been found, some still more or less covered by the skin.

Another though rare means of preserval of the approximately complete animal was shown by the discovery in 1907 of the remains of a prehistoric rhinoceros, unearthed at Bohorodczany in eastern Galicia, Poland. Here are extensive oil and wax mines near which the creature was found at the depth of about six feet below the surface. The head, nasal horn, one of the fore legs, and a large portion of the skin had been preserved in the oil-impregnated soil. We are told that a nearly complete mammoth had been found previously in the same place.

The Yale Peabody Museum contains a remarkable specimen of a ground sloth, *Nothrotherium*, of which the skeleton is still held in articulation by the original tendons and sinews. Several patches of hide are also preserved, one of which is clothed with long yellow hair. This creature was found in a volcanic vent in New Mexico and was buried in accumulated bat guano which

aided in preserving it. Doubtless the skin would be largely complete had it not been devoured by rodents, the marks of whose teeth are still visible. (See Pl. VI.)

Another means of preservation of the animal is in amber, a fossil resin from pines, especially *Picea succinifera*. These resins, which when first exuded are sufficiently soft to engulf a fragile

FIG. 92.—Insects preserved in amber. A, bug; B, aphid; C, caddice-fly; D, may-fly. (After Neumayer.)

insect, later through the evaporation of the more volatile portions become hardened and finally change to amber without the slightest injury to the most delicate details of insect anatomy. About two thousand species, chiefly of insects, but also of crustaceans and spiders, are thus preserved in these Oligocene ambers, as well as over one hundred species of dicotyledonous plants. The so-called "Baltic amber" deposits are found about Königsberg, along the Baltic coast of Samland, Germany (see Fig. 92).

Petrifaction.—As a rule, however, when more or less of the original material is preserved, it has undergone a certain mineralization to which the term *petrifaction* is applied. Naturally the degree of mineralization varies, but is usually greater the older the fossil in time. The parts thus preserved are almost invariably woody tissue or the hard parts of the animal's anatomy—bones, teeth, or shell. Petrifaction implies interstitial addition or an extremely gradual replacement, molecule for molecule, as the original substance is lost through disintegration. The resultant fossil retains, therefore, not only the external form but the histologic characters (*histometabasis*, Gr. ἱστός, tissue, and μετάβασις, exchange) of the original structure as well. Next to the rare preservals by cold or amber, the petrifaction is the most valuable in recompense for careful study. The elaborate exposition of the structure of the fossil cycads by Wieland is based upon this type of preservation, for while in almost every instance in a very large series of specimens the trunk only is preserved, it has been possible by drilling out a cylindrical portion where the buds occur and by cutting it into thin microsections in several planes to reconstruct with entire accuracy the foliage and flowers of the plant (see Pl. VII).

While histometabasis usually occurs with plant tissues, the more perishable soft parts of the vertebrates are, however, occasionally preserved. In one striking instance described by Bashford Dean the muscle fibers and kidney structure are in a state of admirable conservation in an ancient Devonian shark (*Cladoselache*) from the Cleveland shale of Ohio. Microsections of the muscle tissue magnified one thousand diameters show very clearly not only the clean-cut character of the individual muscle fibers, but the cross striation of the skeletal muscles, and in one or two places the delicate membranous sheath or sarcolemma by which the fibers were enclosed.

The replacing substances may be iron pyrites, iron oxide, sulphur, malachite, magnesite, silica, or carbon. Woody tissue, the limy shells of molluscs and the calcareous skeletons of corals and certain sponges are apt to be replaced by silica, giving in some instances a perfect replica of the original in form, though not in minute structure, in a totally different substance, thus forming what is technically called a *pseudomorph* (see Fig. 93). There is evidence that certain hexactinellid sponges the original substance

of which was silica have been replaced by lime, the reverse of what may happen in the calcareous types.

As time goes on, the molecules of the mineralizing substance tend to rearrange themselves according to the laws of crystallography, so that first the minute structure becomes impaired, the external form modified and obscured, and ultimately after an inconceivable lapse of time all trace of the organic original may be lost.

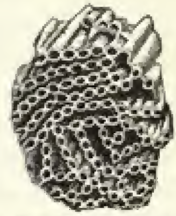

FIG. 93.—Pseudomorph, in which the original lime of the Silurian chain coral, *Halysites catenulatus*, has been replaced by silica. (From Schuchert's *Historical Geology*.)

Natural Moulds and Casts.—Another group of fossils are the natural moulds in which neither the material nor the minute structure is preserved. These are formed by the hardening of the surrounding material in which the organism was buried, followed by the decay and subsequent removal of the organic material by percolating waters, thus leaving a cavity which retains the exact form of the original. In Pompeii, which may in a sense be considered a fossil city, at least two thousand people perished in the eruption of Vesuvius in 79 A. D. The city was covered to a depth of many feet by volcanic ash, finely divided rock which drifted in through the various openings of the houses and buried man and beast as well as the result of man's handiwork. At first when human remains were discovered, the bones were merely dug out and thus preserved; later it was found that if the cavity wherein they lay were filled with liquid plaster of paris the latter would, when hardened, give an admirable replica of the form and features of the victim. The remains of several people, men and women, European and Ethiopian, have been thus reproduced, together with a dog (see Pl. VIII) and the vanished doors and wooden portions of the household furniture.

Some of the fossil vertebrates of the Connecticut valley, which antedate those of Pompeii by millions of years, have lost all trace of the original bone through the percolation of dissolving waters. The impression, however, still remains, by means of which a fairly perfect restoration of much of the skeleton may be made.

Often these moulds are filled in with other material, so that a natural cast of the object is formed differing from the petrifaction in that it retains the form of the organism but not its structure. By this means such evanescent things as jellyfishes have been pre-

served. Again, interior cavities, as of shells or the brain chamber of a vertebrate skull, may be filled with subsequently hardening sediment, so that a perfect cast of long vanished soft parts is produced. This in the case of shells is often deceptive and has led to some confusion and duplication of names because of the striking dissimilarity of the outer and inner surfaces of the same shell. In the vertebrates, however, the brain replica is of the utmost importance, for form, size, and proportions of parts are all preserved with absolute fidelity. It is, however, a cast of the dura mater or outer membrane of the brain, and while blood-vessels and nerve roots are often clearly indicated, the depth and complexity of the minor convolutions are not recorded.

Footprints and Trails.—A certain group of phenomena should be considered in this connection—the footprints and trails of verte-

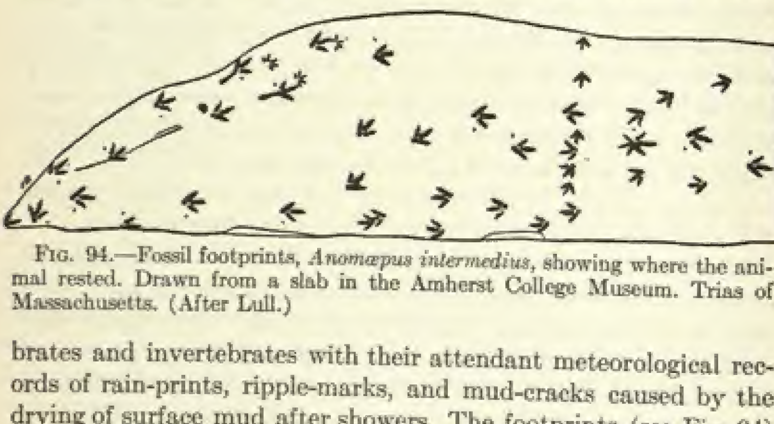

FIG. 94.—Fossil footprints, *Anomœpus intermedius*, showing where the animal rested. Drawn from a slab in the Amherst College Museum. Trias of Massachusetts. (After Lull.)

brates and invertebrates with their attendant meteorological records of rain-prints, ripple-marks, and mud-cracks caused by the drying of surface mud after showers. The footprints (see Fig. 94) are of double interest, for not only are they oftentimes so well preserved as to enable the student to trace much of the structure, but they sometimes give a clue to the proportions of the entire animal, especially when to the impressions of the hind feet are added those of the hands and tail. Furthermore, the footprints bring before the observer more clearly than any other records of the past the individuality of the creature, for they are fossils of *living beings*, while all of the other relics are those of the dead.

Coprolites.—A clue to feeding habits is generally gained from the study of the mouth armament in comparison to that of living allies, but conclusions are sometimes verified and supplemented by finding the fossil rejectamenta in association with bones or foot-

prints. To such relics the term *coprolite* is applied. Sometimes the unvoided intestinal contents preserves the outline and extent of the alimentary canal. This is distinctly seen in several of the salamandrine forms preserved in Carboniferous nodules from Mazon Creek, Illinois.

Conditions for Fossilization

Immediate burial is the first prerequisite for fossilization and it should be such as to exclude the air so as to prevent oxidation of the organism. This burial is most often effected by water-borne sediment, which in turn is derived from the degradation of older rocks. Sediment deposited in the seas and oceans is of the first importance, and as a consequence the fossil remains of creatures making their home in the shallower regions are by far the most abundant, while the deep-sea organisms are comparatively unknown because so little of these deposits has been elevated into land. The first-named deposits, especially when formed near the mouths of rivers, sometimes contain the remains of land or fresh-water animals which were swept out to sea by the stream, but such inclusions are purely accidental and not of common occurrence; in some instances, however, notably in certain dinosaurs, they have given us the only specimens of their kind thus far discovered.

Fresh-water deposits are largely those of river bar or delta or flood-plain, though ponds and lakes do add their quota. The great Tertiary fossil fields of the western states were formerly supposed to be the result of lake-borne sediment, but the lakes would have been of such vast extent that the creatures in many instances were found an impossible distance from the supposed shore-line, where burial would be ineffectually slow. The lacustrine theory of origin has therefore been largely abandoned in favor of the idea of flood-plain sediments of ancient rivers. The greater part of our knowledge of terrestrial vertebrates is derived from such deposits.

Wind-borne material in the form of loess or volcanic ash has yielded fossils of land-living beings, the former containing largely shells, while the bones of the vertebrates are more often found buried in the latter; the sloth mentioned earlier in the chapter was preserved in an accumulation of bat guano.

Miring.—Miring in bogs and quicksands, with its combined death and burial, has been a mode of preserval which has notable

examples in the mastodons found in numbers in New York and the adjacent states, and the great Irish deer whose remains are common in the peat bogs of Ireland.

Perhaps the most remarkable death trap in the world is found in the Rancho La Brea which lies on the western border of the city of Los Angeles, California. The conditions there are thus described by Miller, after Merriam:

"Crude asphaltic oil from the underlying Fernando shales . . . has been forced to the surface through cracks or chimneys in these folded strata to accumulate upon the surface as more or less extensive oil pools. This heavy oil, under the influence of sun and wind, underwent a process of natural distillation, becoming more and more viscid until in the larger accumulations it was sufficiently tenacious to entrap and hold the largest mammals of the region, *Elephas*, *Mastodon*, and *Paramylodon* [*Mylodon*]. . . . Additions of these lenses of asphalt took place at the center as fresh oil rose through the chimneys from below; at the same time dust and sand drifted over and obscured the firmer asphalt of the margins. These two factors combined to bring about a most deceptive condition in the mass by leaving the periphery fairly firm and yet permitting a gradually increasing degree of plasticity toward the center without a positive demarcation of the danger zone. Upon this treacherous surface a mammal would be unaware of danger until the dust-covered surface yielded under his weight. His sudden start or his leap for safety would make all the more complete his entanglement. . . .

"The entanglement of one ungulate would suffice to attract a multitude of carnivores. The creature probably acted not infrequently as live bait for a considerable time, so that its struggles and outcries served to whet the appetites and overcome the instincts of caution in the hungry carnivore. It appears from Merriam's studies that young animals or else old and diseased individuals have very frequently been thus tempted, though there appear animals of all ages."

Subsequent Vicissitudes.—After all of the conditions for initial preservation have been fulfilled, the resultant fossil is subject to various vicissitudes as time goes on, due to pressure, elevation, folding, and subsequent erosion of the strata, and to the slow circulation of acidulated and other waters through the rock, either from above or below. The latter may dissolve away shell or bone,

leaving only a mould which may be subsequently obliterated, or the mineralized fossil may assume a crystalline structure and thus become unrecognizable as a relic of organic life.

Crushing is due not alone to the tremendous weight of the superposed rock, but also to the natural shrinkage of water-laid sediment in the subsequent drying-out process to which it is subjected. Notable instances of such distortion are shown in the Niobrara chalk of Kansas, which was laid down in a shallow inland sea toward the close of Cretaceous time. Here the bones of *Pteranodon* and other winged reptiles are crushed flat, though formerly those of the limbs were cylindrical, but very thin-walled. In one specimen of a mosasaur preserved in the Yale Museum the vertebræ had originally an average length and breadth of about 80 mm.; one of these vertebræ which lay upon the articular face has a present length of 21 mm., while another which lay upon its side has had its breadth reduced in the same ratio, about 1:4.

Sometimes the fossil has been subjected to an oblique shearing movement which completes the distortion, and it requires the most judicious study to restore the organism mentally and graphically to its original symmetry of form.

Field Technique

In his search for fossil shells and plant remains one need not go far afield, for wherever sedimentary rocks are exposed there is a varying chance for success. The fossils in which the more fragile portions of the organism are preserved are not so often met with and but few areas the wide world over have thus far produced them. Terrestrial vertebrates are also rare as to localities, though often abundant within a limited area or horizon. Aside from certain places where fossil-bearing rocks have been brought to light as a by-product of some commercial enterprise—mine, quarry, or railroad cutting—the most productive exploration has been made in the drier areas of the globe where soil or glacial drift does not conceal the eroded rocks and where the whole geologic structure is unobscured by a mantle of vegetation. Thus the semi-arid portions of our West, of Patagonia, or of northern Africa and central Asia are among the most favored places for field research.

The vertebrate technique has been reduced to a science, which may be briefly summarized. After a judicious questioning of the inhabitants of a given region, which often yields much information

of value, the prospector, acting upon the knowledge thus gained, begins a careful, systematic search of the exposed rock, generally along cliff or escarpment, or within eroded water courses. Here one may see some portion of the skeleton protruding from the sandstone, or the first indication may be a fragment underfoot, technically called a lead, which one must if possible trace up the declivity until its original resting place is found. This may reveal the more or less complete skull or skeleton of a bygone type. Upon locating his prospect the worker then excavates the specimen with the utmost care, hardening it if necessary with weak shellac or a solution of gum arabic, which permeates the bone and renders it capable of being handled where otherwise it might be too fragile to save. The joints which are found in all consolidated rock often pass through the specimen, rendering it already in fragments while still in its native matrix. Hence as the bone is exposed from above it is covered with strips of cheesecloth or burlap dipped in flour paste for the smaller specimens or in liquid plaster of paris for the larger. When these bandages have thoroughly dried the fossil is further excavated and the covering extended until it is so far protected that one may completely undermine it and lift it from its bed. The bone is then turned over and the bandaging completed. In the case of a large bone or skeleton, wooden splints are included within the outer bandages, the process being analogous to the treatment of a fractured limb by a surgeon; in fact, it was a physician who first adapted the surgical method to the collecting of fossils. Careful labeling, packing in specially constructed boxes in hay or straw, and transportation to the museum, which often implies a long haul or portage before the railroad is reached, complete the work of the collector.

In the museum the preparators unpack, and by softening the bandages with water they are one by one removed until the fossil is laid bare. Then the matrix is carefully removed, the bone further hardened with a suitable solution, all fractures repaired with a preparation of plaster of paris and glue, or other special cement, and the bone is ready for study.

Significance of Fossils

As one has said, the laws of physics are unchanging with the flight of time. A crystal formed a million years ago is precisely similar to one formed yesterday. Organisms, on the other hand,

are not immutable, but are continually evolving into other and more specialized forms, though the rate of progress may be retarded or accelerated, and a given race of animals or plants may differ markedly from another in its plasticity. Nevertheless the law holds true that mineral forms are changeless, whereas organic forms are altered as time goes on. Thus it comes to pass that while the nature of a given rock and that of its contained minerals may give no possible clue to its geologic age, the character of the included fossils indicates conclusively the time when the sediments were laid down. Certain types of animal or plant life are so characteristic of certain geologic horizons that the term index or guide fossils has been applied to them, and their importance in ascertaining geological chronology is of the first order.

Fossils indicate the extent and boundaries of former lands and waters, the marine fossils showing the limits of encroaching seas, those of terrestrial origin the continental areas, the two combined defining with great nicety the ancient coast lines as interpreted by the expert. Further, as the isolation of contemporary marine faunas implies the existence of land barriers, so the appearance of new terrestrial animals previously unknown within the area is evidence of the formation of new land-bridges to serve as paths of migration. It was such evidences as these which enabled Professor Schuchert to prepare the admirable series of maps showing the evolution and vicissitudes of the North American continent and thus to raise Paleogeography to the status of a science.

The variation of temperature and degree of moisture is perhaps most clearly indicated by the fossil plants, but at the same time the animals do add their evidence; for instance, the increasing aridity in the West during the Tertiary, had we no remains of the flora, would be as emphatically proved by the rapid diminution in the number and kinds of browsing animals and the great increase of grazing forms after the beginning of the Miocene.

The modern camels show perfect desert adaptations which include, among other details, the yielding, padded foot. The earlier camel-like forms have deer-like feet. The retrogression into the typical foot of the camel therefore indicates the beginning of desert adaptation and hence of aridity of climate.

The study of fossils has given rise to a new branch of Zoölogy and Biology, and while it cannot be carried to the extent of an experimental science, the growing wealth of knowledge which

Paleozoölogy embraces could be studied by the laboratory biologist with great profit.

A student of the philosophy of history may gain much knowledge whereupon to erect the fabric of his theories by his own observation of contemporary events; but for final proof of his deductions he turns to musty records of the bygone centuries wherein he may trace the evolution of nations and the rise and fall of empires.

So it is with the student of evolution, concerning which a great deal can be learned by experimental work, by the propagation of domestic animals and plants, and by witnessing the wonderful adaptations to every possible environment on the part of the teeming hosts of living forms. But as with the human historian, the final proof rests upon the documentary evidence which in this instance Paleontology alone can furnish. This evidence is still imperfect in parts, the chapters were never written in others, or the record has suffered grievous mutilation by the relentless hand of time. In places débris from the older rock with its contained fossils has been redeposited, confusing the record, as a palimpsest may show traces of former writings intermingled with the new. In spite of these vicissitudes the evidence is becoming more and more complete, and with each added link the vision of him who contemplates it grows ever clearer.

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CHAPTER XXVI

CEPHALOPODS

Place in Nature.—Disregarding for the present the great subkingdom Protozoa, animals have followed three great evolutionary lines, culminating in the molluscs, the arthropods, and the vertebrates; of these the cephalopods represent the final goal of molluscan evolution, the insects of arthropod evolution, and the mammals of vertebrate evolution. Of all the invertebrate groups, therefore, the cephalopods and insects will prove the most instructive subjects for our inquiry.

The Cephalopoda are the most highly specialized molluscs, related to the humbler, more or less sedentary bivalves, clams, oysters, etc., and to the somewhat more ambitious univalves, the snails, whelks, and periwinkles. The cephalopods themselves include the free-swimming squids, cuttle-fishes, octopi, argonauts, and nautilus, and a host of extinct shelled forms allied to the last and representing a large group of which it is the sole survivor.

In general the cephalopods are divided into two principal sorts, the one aggressive, swift, well armed but not armored—an essentially modern animal; the other sluggish and armored—old-fashioned in every sense of the word. An example of the first would be the squid *Loligo*, of the second, the pearly nautilus, *Nautilus*. An understanding of the essential structure of these two types is necessary.

Structure

Squid

Head and Arms.—*Loligo pealii*, a squid, is a bilaterally symmetrical animal, having a distinct head, which protrudes from the open end of the conical mantle enclosing the body. This is elongated and tapers toward what appears to be the posterior end. There are a pair of horizontal fins at this end which together are more or less rhombic. The head is embellished with a pair of large, well developed eyes, and bears eight long tapering arms, forming a circle around the mouth. There are two additional grasping

tentacles capable of a considerable degree of extension. The arms bear on their inner face rows of suckers for adhesion; on the extensile tentacles these are borne only on the expanded tip, on the others throughout practically the entire length.

Suckers.—The suckers are goblet-shaped, each consisting of a shallow cup borne on a short stalk, having a membranous lip, within which is a narrow horny rim with a serrated margin. Within the cup is a muscular plug or piston arising from its bottom. When the sucker comes in contact with any object to which the squid wishes to cling, the horny rim is pressed against it and the membranous lip hermetically seals the joint. Then the piston contracts,

FIG. 95.—Squid, *Loligo* sp., capturing a fish. (After Doflein.)

producing a partial vacuum within the cup which causes it to adhere very strongly through the pressure of the surrounding water.

Siphon.—Beneath the head lies the siphon or funnel which, as we shall see, constitutes, together with the mantle, the principal organ of rapid locomotion. The mouth, which is in the center of the circle of arms, possesses a powerful beak, like that of a parrot except that the lower jaw overlaps the upper. Within the mouth is a muscular tongue armed with a flexible rasp-like organ, the radula, a structure found also in the snails.

Mantle Cavity.—The mantle, which is derived from the body-wall and is characteristic of all molluscs, encloses not only the body but a cavity of considerable extent along the under side almost to the apex. This, the mantle cavity, is in communication with the surrounding water through the free edge of the mantle itself; and also by means of the funnel which has already been mentioned and which is a tapering tube with its wider end opening into the cavity, its narrower one into the outside water.

Within the mantle cavity are seen the respiratory organs—a pair of plumose gills—and it also receives the wastes from the alimentary canal, the kidneys, and other organs. The rhythmic ebb and flow of water from the mantle cavity carries off these wastes,

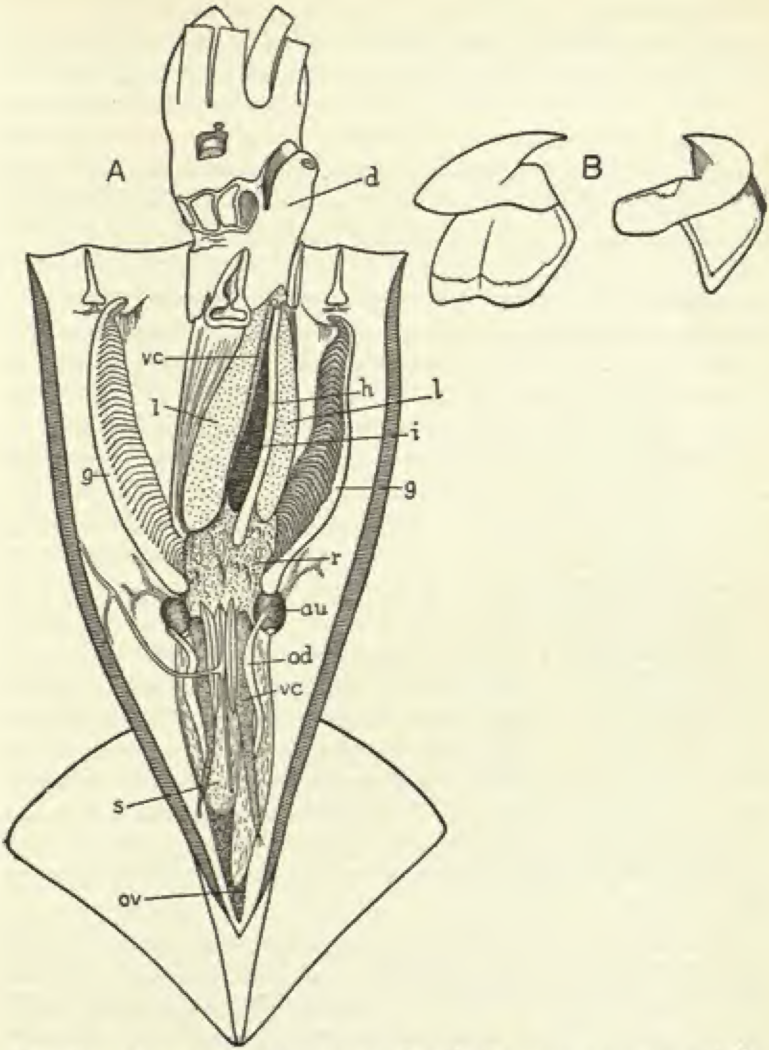


FIG. 96.—A, anatomy of female squid, with the arms cut away and the mantle slit open and pressed aside: *au*, branchial auricle; *d*, funnel; *g*, gill; *h*, intestine; *i*, ink-sac; *l*, liver; *od*, oviduct; *ov*, ovary; *r*, renal organ; *s*, blind sac of stomach; *vc*, vena cava. B, jaws of squid. (After Verrill.)

brings fresh water for respiration, and also subserves the function of locomotion.

Locomotor Organs.—Locomotion is effected in three different ways: either by crawling on the tentacles, by swimming forward by means of the fins, or, more rapidly, in a backward direction, by forcing a series of strong jets of water out of the mantle cavity through the forwardly directed funnel. This last is accomplished by the rhythmic relaxation of the muscular mantle, during which water flows into the cavity all around the neck; then the neck portion contracts so that the only exit is through the narrowing funnel, and a forcible contraction of the entire mantle forces the water out. The fins must act merely as keels during this backward progress, and the arms trail in the creature's wake as rudders. When the extensile tentacles are contracted and the other arms pressed closely together, the squid shows a fish-like contour like that of other swiftly swimming aquatic types, with the greatest diameter about one-third of the length from the apex, which in rapid progression thus corresponds to a fish's snout. One form, *Ornithoteuthis volatis,* the flying squid, can leap from the water and, like a flying fish, occasionally land on the deck of a vessel.

Ink-sac.—One remarkable organ which has not been mentioned is the ink-sac (see Fig. 96), a pear-shaped body, the interior of which is glandular and secretes a black substance known as the ink or sepia which collects in the cavity of the sac. This communicates by means of a duct with the mantle cavity, so that, if the squid is startled, the ink is poured into the cavity, where it mingles with the water, forming a dense black cloud when forced into the surrounding water, under cover of which the creature escapes (see Fig. 109). This is analogous to the smoke screen used by ships in time of war.

Sense Organs.—In common with all well-developed motor types, the sense organs and nervous system are highly evolved, and the latter is protected by a capsule of cartilage analogous to the vertebrate cranium. The eyes have been mentioned and they are splendid structures comparable in their degree of perfection to those of the vertebrate, although of course entirely independent in their origin and development. Ciliated pits behind each eye are also the seat of a well-developed special sense which has been interpreted as that of smell, and in addition there are organs of equilibration known as otocysts. These were formerly supposed to be

organs of hearing, but such a function is entirely unproved; on the other hand, their removal leads to the loss of balancing control. Luminescent organs are found in certain of the squids, notably the flying squid mentioned above, which can project a clear light from the axis of every arm.

Shell.—The vestigial shell is reduced to a horny or chitinous body having much the shape of an old-fashioned quill pen. It lies along the back of the animal in a pocket-like depression in the mantle, and thus serves to stiffen the creature after the manner of an internal skeleton.

Color.—The color of the squid is variable, owing to the development of chromatophores (see page 196), pigment cells which are capable of expansion and contraction and thereby diffuse or concentrate the color as the case may be; thus flushes of different hues pass over the body of the animal, allowing it to conform with the environmental coloring.

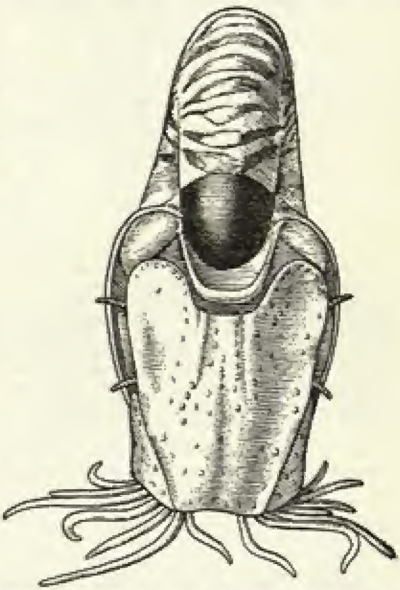


FIG. 97.—Nautilus adhering by means of its tentacles. (After Willey.)

Nautilus

While squid-like cephalopods are numerous, the nautilus is very rare, for but four species of the genus now exist, and these are all the living representatives of a formerly large and dominant race. At present the nautilus inhabits Oceanica from the Malay to the Philippine and Fiji islands, living at depths varying from 300 to 600 feet, although they have been taken at 1000 feet. They are never found at the surface except when dying, but their empty, chambered shells, which are very buoyant, are carried long distances by waves and ocean currents.

Comparison with Squid.—The coiled, chambered shell, in the outermost portion of which the creature lives, is the most distinctive thing, but in still other ways the nautilus differs from the

squid, for example, in having four gills instead of two, and, in the female, ninety tentacles instead of eight or ten. Good authorities have supposed that the many tentacles of the nautilus are not homologous with the arms of the squid, but rather with the suckers which they bear. In certain ancient squid-like forms (*Acanthoteuthis speciosa*) from the Jurassic limestone of Eichstädt, Bavaria, the arms bore hook-like processes instead of suckers, which lends weight to this idea. The nautilus has an imperfect funnel in that the two margins of the scroll are not united, so that the organ can be unrolled and used for crawling. It is therefore in a more primitive condition. The eye also is much more primitive, for instead of being a highly developed optical instrument, it is devoid of lenses, having merely a pinhole-like aperture to admit the rays of light. Such an organ does, however, form an image upon the retina, but it is indistinct in detail like an impressionist picture. The nautilus is a voracious carnivorous type, but cannot compare with the swift, aggressive character of the squid, for the former crawls over the sea-bottom or swims jerkily along, and it will be seen at a glance that it is not built for speed.

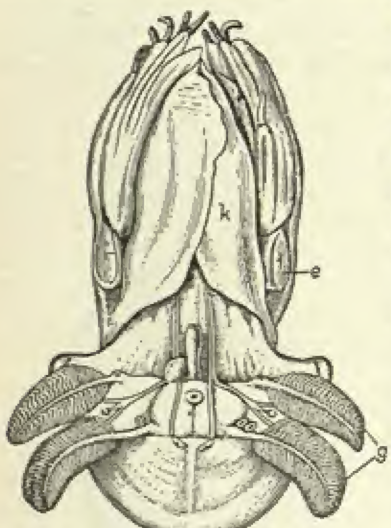


FIG. 98.—*Nautilus pompilius* removed from shell to show anatomy: *e*, eye; *g*, gills; *k*, funnel. (After Willey.)

Shell.—The shell is a beautiful structure formed internally of mother-of-pearl, overlain with a striped porcelanous layer. The chambers are separated by thin pearly transverse partitions known as septa, which the animals secrete at regular intervals after moving forward a short distance in the living chamber. These septa are concave outward and are pierced by a circular aperture continued backward into a small funnel (septal neck). Through this funnel passes a fleshy siphuncle arising from the rounded hinder aspect of the animal and continuing throughout all of the chambers to the tiny innermost one, where it is fastened to the inner side of

the wall. By means of this siphuncle the inner chambers may be charged with a nitrogenous gas to render the shell more or less buoyant, so that it is not at all burdensome to the animal.

In primitive forms the shell was a straight cone (*Orthoceracone*), lying in the original dorso-ventral axis of the animal; subsequently it became coiled (*Cyrtoceracone*, *Gyroceracone*, *Nautilicone*), and

FIG. 99.—Chambered nautilus, *Nautilus pompilius*, in natural position, the shell sectioned. *a*, mantle; *e*, eye; *f*, horny girdle for adhesion of mantle to shell; *k*, funnel; *n*, hood; *p*, protruded tentacles; *s*, siphuncle for communication with inner chambers of shell. (After Owen.)

in racially old types its coils loosen and it once more becomes straight, with the exception of the embryonic shell, which retains its ancestral coiling.

Suture Line.—The septa are firmly united to the sides of the cone, the line of union, which is straight or curved, sometimes forming a highly complex series of infoldings. This line is called the suture, and is not visible from without in recent shells, but in fossils the outer shell is often lost and thus the sutures become plainly discernible. They form criteria of great taxonomic importance.

Nautilus possesses no ink-sac.

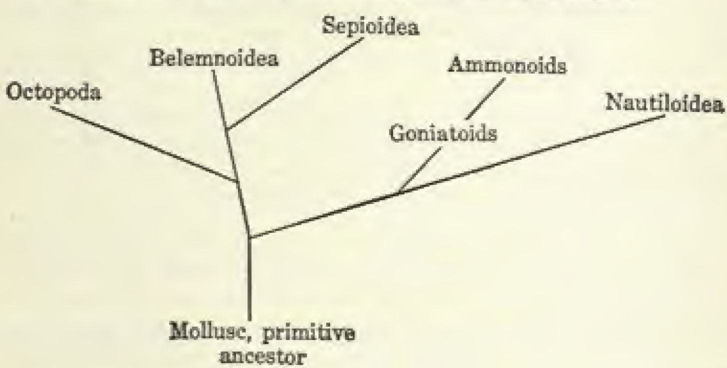
CLASSIFICATION

The following scheme will render the classification of the cephalopods clear:

Class Cephalopoda

Subclass **Tetrabranchiata**[1] (4-gilled) Shell external, a chambered cone; no ink-sac.		Subclass **Dibranchiata**[1] (2-gilled) Shell internal or none; ink-sac.	
Order **Nautiloidea**	Order **Ammonoidea**	Order **Octopoda** (8-armed).	Order **Decapoda** (10-armed).
Shell primitive, with simple sutures, not highly ornamented.	Shell progressive, with complex sutures, highly ornamented.	*Argonauta.* Male shell-less; female with external shell. Unchambered. *Octopus.* Shell-less.	Suborder **Belemnoidea**[2] *Belemnites.* Internal shell, partially chambered. *Spirula.* Internal shell wholly chambered. Suborder **Sepioidea** Internal vestigial shell. *Sepia*, cuttlefish. *Loligo*, etc., squid or calamary.

The classification may be expressed diagrammatically as follows:



[1] These terms, which are in common usage, are objectionable, as we really have no direct knowledge of the gills of the extinct ammonites. Alternative terms which meet this objection are Ectocochlea (external shell) and Endocochlea (internal shell).

[2] Abel has shown that the belemnites had but six arms, and if so the term Order Decapoda does not properly include them. Their relationship to the Decapoda proper is, however, admitted.

Subclass Tetrabranchiata (Ectocochlea)

These are nautilus-like forms presumably with two pairs of gills and with a well-developed shell in the form of an elongated, chambered cone which later becomes coiled and then, in racial old age types, uncoils again. In size they do not as a rule compare with the larger of the dibranchiates, and yet certain individuals of the ancient straight-shelled *Endoceras* had a shell at least 15 feet long.

Geological History.—The tetrabranchiates, on account of their resistant shell, are much better known geologically than are their more modern relatives, the dibranchiates, so that their evolutionary history as told by the shell has been worked out in detail. Schuchert summarizes the shell changes of the nautiloids thus:

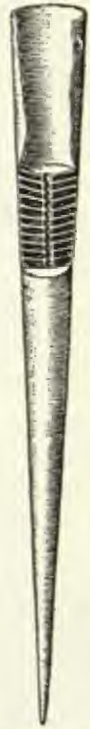


FIG. 100.—*Orthoceras* shell. (From Schuchert's *Historical Geology*.)

"Nautilids appeared in fair abundance in the Lower Ordovician. Among these the most primitive were straight, tapering cones that were circular or oval in outline, and because there are many families of them they are called *Orthoceracones* (from the genus *Orthoceras* [Fig. 100], meaning *straight horn*). These orthocerids were common throughout the Paleozoic and particularly so in the Ordovician and Silurian. . . . With the Devonian these primitive forms began to wane slowly, but some were still present in the Triassic. All other types of cephalopods had their origin in the straight-shelled Orthoceracones and the first of these had their cones slightly bent and are therefore called *Cyrtoceracones* (from *Cyrtoceras*, meaning *bent horn*); later descendants were coiled in a loose spiral wound in a plane and are known as *Gyroceracones* (from *Gyroceras*, meaning *round horn*); still others are tightly, wound, with the whorls embracing one another more or less closely, as in *Nautilus*, and these are termed *Nautilicones*. On the sides of such one sees more or less of the inner whorls of the shells, and the area of these whorls is spoken of as the *umbilicus*. It is small in *Nautilus* and wide or open in the Ordovician forms. The bending of the tubes

is due to a more rapid secretion of lime along the ventral side of the cone, and the greater the unequal growth, the more rapidly the cone . . . rolls up," or becomes involute.

The geologic record of the evolution of the Tetrabranchiates includes of course the two main suborders, Nautiloidea and Ammonoidea. The first were long-lived, ranging from Cambrian time until the present. They embraced, however, several parallel phyla, but their long life is due in part to the fact that the degree of specialization to which they attained was never very great. Of the ammonoids, on the other hand, the reverse is true, for as their specialization was high, so was their career brief and rocket-like—swift in its ascent, dazzling in the culmination into many beautiful and remarkable forms, and headlong in the descent into oblivion. It must be borne in mind, however, that in using such a figure of speech we are speaking relatively, for the career of the ammonites, extending as it did from the Devonian to the close of the Cretaceous, was really of immense duration.

Fig. 101.—*Cyrtoceras* shell. (From Schuchert's *Historical Geology*.)

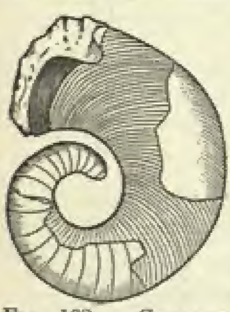


Fig. 102. — *Gyroceras* shell. (After Zittel.)

Fig. 103.—*Lituites* shell. (After Zittel.)

Nautiloids.—The first undoubted cephalopod known is of latest Cambrian age, and belongs to the *straight-shelled* Orthoceracone type which is the radicle of the group. *Endoceras*, the most primitive of orthoceran forms, prevailed in the Ordovician, but here came in also curved forms, at first sparingly, then later abundantly. The simple unspecialized orthoceran type survived throughout the entire Paleozoic, and finally disappeared near the end of the Trias.

The first of the *curved* forms departed little from their ancestral habit, but enough to give a new generic title, *Cyrtoceras* (Fig. 101).

Cyrtoceras is Ordovician to Devonian in distribution. As time went on the curving became more pronounced. Finally the coil became complete, though the successive whorls did not touch the preceding ones; this stage is called *Gyroceras* (Fig. 102) and is most commonly Silurian in age. Later the succeeding coils began to touch and finally to embrace the preceding and the culmination of nautiloids was reached in *Nautilus* (Fig. 99).

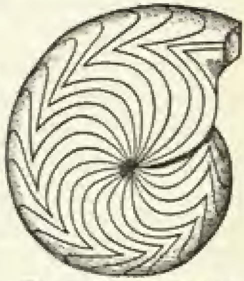


Fig. 104.—Goniatoid shell. (From Schuchert's *Historical Geology.*)

When the close-coiled stage was attained the nautilian shell had reached its limit and could progress no farther, and at once some of the stock began to retrograde, and uncoiling shells appeared. *Lituites* went through the orthoceran, cyrtoceran, gyroceran, and nautilian stages, and as it became adolescent left the close coil and reverted to the orthoceran stage (see Fig. 103). It is of middle Ordovician age.

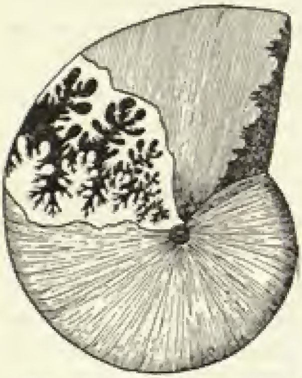


Fig. 105.—*Phylloceras* shell. (After Zittel.)

The reversionary nautiloids are confined to the early and middle Paleozoic and did not in any case become radicles of later groups; they had run their course and exhausted the possibilities of development, and died out without descendants. The old simple orthoceran shell, however, held out until the Trias, and then gave rise to the belemnoids, and the unspecialized nautilian shell endured until the present time, though now rapidly nearing extinction.

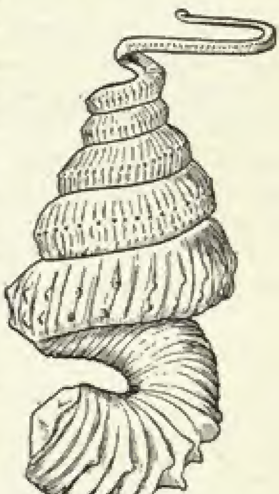


Fig. 106. — *Heteroceras* shell. (From Schuchert's *Historical Geology.*)

Ammonoids.—The ammonoid ancestor is represented by *Bactrites*, an orthoceroid which by acceleration of development acquired a calcareous protoconch or embryo shell, and a marginal or ventral siphuncle. The ammonoid line appears in the Ordovician. By Devonian time they have sutures bent or fluted into lobes, and narrow shells, and it was out of this stock that the true ammonoids developed early in the Carboniferous.

From the Nautilinidæ of the Silurian the cephalopods of the Devonian branched out rapidly, continued increasing and diverging in the later Paleozoic, and in the Mesozoic became highly specialized and accelerated until their final extinction at the end of Cretaceous time. In the Jura these ammonites reached their acme, branching out into very many families and subfamilies, increasing usually in complexity of sutures and variety of ornamentation. In the Cretaceous they gradually declined, dropping off one at a time until all were gone.

Only a few stocks persist in the Cretaceous, but from time to time during this period certain genera branch off from the main stock, become highly specialized and often give rise to so-called abnormal forms, phylogerontic or degenerate genera (retrogressive), which do not perpetuate their race. These change their close coil, becoming straight as in *Baculites*, ascending spiral as *Heteroceras* (Fig. 106), hook-shaped as *Hamites*, or open-coiled gyroceran as *Crioceras*. These do not form a natural group, but are themselves in some cases polyphyletic, as is apparent from their ontogeny.

The following table expresses in graphic form the evolution of the tetrabranchiates.

Recent Quaternary		Nautiloids 2500 spp. Nautilus living 4 spp.		Ammonoids 5000 spp.	
Tertiary	Conditions less favorable				
Cretaceous				Final total extinction General retrogression	Unfavorable conditions
Jurassic			No uncoiling types	Great numbers — Progressive Second maximum — Retrogressive	
Triassic	Unfavorable conditions	Gradual decline		First uncoiling types First maximum	
Permian				Marked progressive evolution	
Carbon-iferous		Sharp decline		Progressive evolution	
Devonian			Uncoiling types	Progressive evolution begins	
Silurian	Favorable conditions	Maximum			
Ordovician			Uncoiling types *Lituites*	Appear as goniatoids.	
Cambrian		Appear ?			

Subclass Dibranchiata (Endocochlea)

The dibranchiates may be diagnosed as follows: Active, unarmored cephalopods with two gills; funnel complete; ink-sac usually present; with six or eight (Octopoda), or ten (Decapoda) arms provided with suckers or hooks. The vestigial shell generally reduced and sometimes wanting, always internal. Relatively modern types.

Belemnoids.—We cannot trace the evolution of the modernized dibranchiate cephalopods with the same assurance as that of the

tetrabranchiates, because of the gradually diminishing shell which reduces proportionately the chance for their preservation as fossils. Belemnoids are, however, well known and render possible an understanding of the evolution of the shell. In this group, which is characteristic of the Mesozoic, the mantle had become more and more external to the shell so that the latter came to lie within its substance. Hence the shell has more the character of an internal skeleton than of a protective armor. The belemnoid shell (see Figs. 107, 108) is straight, conical, and chambered; the septa are close to one another and are perforated toward the ventral side of the shell by a very slender siphuncle. The posteriorly directed apex of the shell, the phragmacone (see Fig. 108), is protected by a calcareous sheath or guard, usually the only part preserved. The anterior wall of the last chamber is prolonged forward on the dorsal side into a broad, thin process, the proöstracum. Of these parts the phragmacone is of historical significance since it is clearly derivable from the shell of the Paleozoic orthocerids, out of which, in the early Triassic, the belemnoids arose.

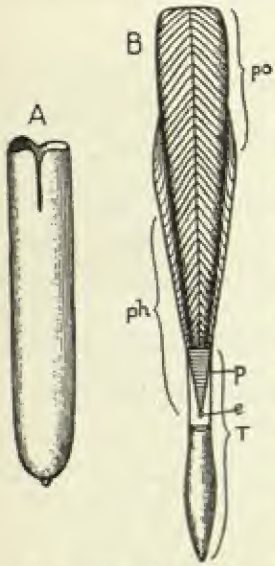


FIG. 107.—Belemnoid shell. A, guard, part commonly preserved. B, entire shell: *e*, embryonic or first shell; *p*, chambered phragmacone, passing upward into the limy or chitinous phragmacone (*ph*); *po*, proostracum; T, solid guard or rostrum; cut to show phragmacone. (After Steinmann, from Schuchert's *Historical Geology*.)

An interesting form is *Spirula* whose shell (shown in Fig. 108,D), coiled into a loose spiral, represents the phragmacone only, the rostrum having disappeared. *Spirula* was formerly supposed to be unique in being the only known sedentary cephalopod. During the recent expedition of the ship "Michael Sars," however, 95 living specimens were secured and their habits observed in an aquarium, with the result that, instead of being sedentary, *Spirula* is now seen to be pelagic, floating head downward and hovering in the intermediate depths far from the bottom.

The **Sepioidea,** another group of Mesozoic dibranchiates, retained only the proöstracum and the completely modified remnant

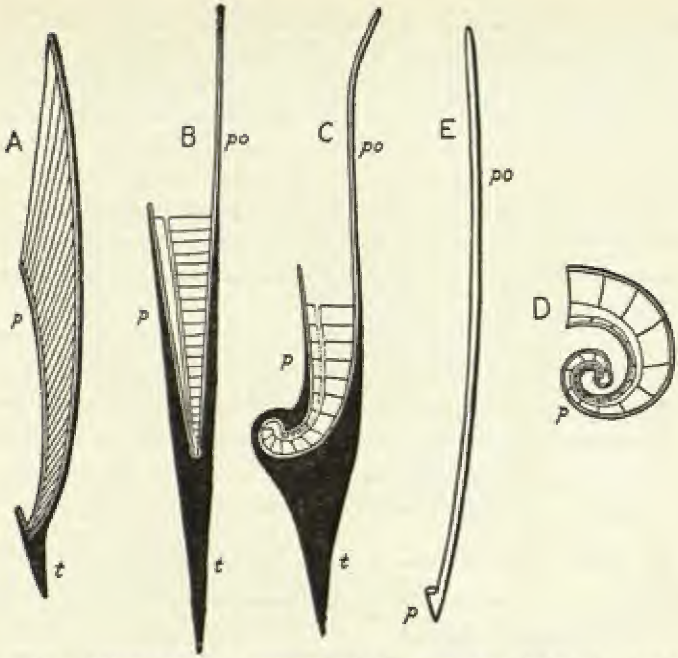


FIG. 108.—Diagrammatic sections of dibranchiate shells. A, *Sepia;* B, *Belemnites;* C, *Spirulirostra;* D, *Spirula;* E, *Ommastrephes;* p, chambered phragmacone; po, proöstracum; t, rostrum. (After Lang.)

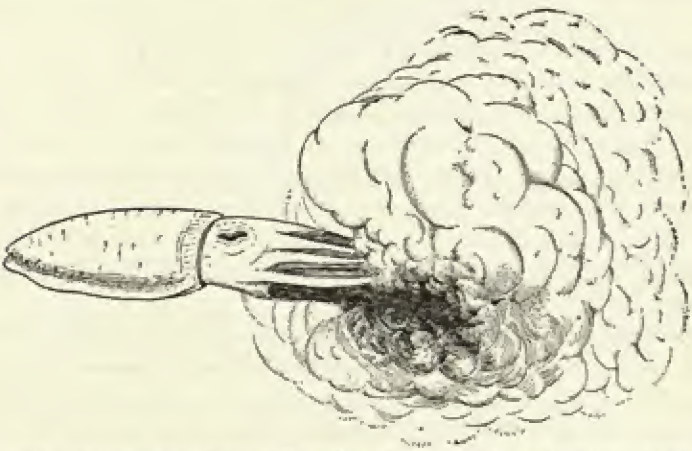


FIG. 109.—Cuttle-fish, *Sepia officinalis*, discharging its protective cloud of ink. (After Doflein.)

of the phragmacone, which combined to form a wide and thick but very light and porous "bone," consisting of delicate plates of lime separated by vertical fibers. These shells are characteristic of the cuttle-fish, which range from the Jurassic (Oxford Clay) to the present. Some of the Upper Jurassic forms had a cuttle-bone at least two feet in length, indicating a creature from six to eight feet long (see Fig. 108,A). The proöstracum, projecting toward the head of the Mesozoic squid, has become a structure known as the pen, and in some living genera such as *Ommastrephes* and *Loligo* the pen alone remains.

The modern genus *Architeuthis* (Fig. 110), the giant squid, is the fitting culmination of this evolutionary line, for some of them are not only the largest of invertebrates, but, when measured to the tip of the extended tentacular arms, exceed the length of any known

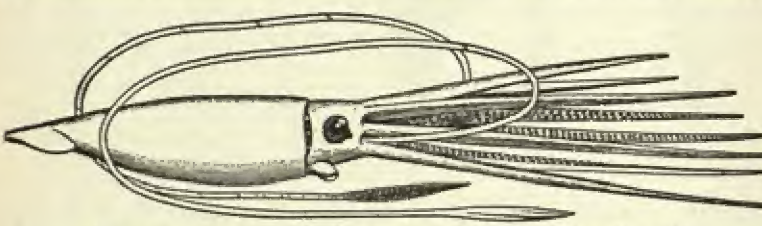


FIG. 110.—Giant squid, *Architeuthis princeps*. (After Verrill.)

vertebrate except the larger whales and the amphibious dinosaurs. The body may be as large as a hogshead and the extreme length of body and tentacles may exceed half a hundred feet.

Octopoda.—In the eight-armed dibranchiates the extreme of specialization is reached, for the internal shell has entirely disappeared and but one of the groups, the female *Argonauta* (Fig. 111) (the male (see Fig. 17) being shell-less), has anything comparable to such a structure. Here the unchambered shell is more in the nature of a brood chamber and as such not homologous with the shell either in the Decapoda nor yet in the tetrabranchiate Cephalopoda.

The fossil record of the Octopoda is almost entirely blank, hence their evolution may not be traced. The most ancient octopus, known as *Calais*, comes from the Upper Cretaceous of Mount Lebanon, Syria, while the argonauts are unknown before the Tertiary.

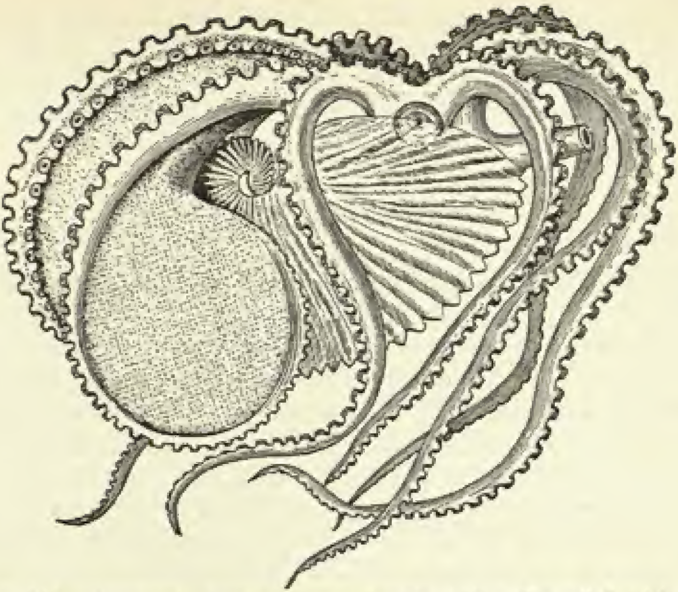


Fig. 111.—Argonaut, *Argonauta argo*, female. (After Claus-Sedgwick. For male see Fig. 17.)

Fig. 112.—Swimming octopus, *Octopus* sp. (After Doflein.)

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CHAPTER XXVII

INSECTS

Place in Nature.—As the cephalopods are the culmination of the evolution of the unsegmented invertebrates, so the insects can be considered the final evolutionary goal of those whose bodies are segmented, the so-called "Articulates" of Cuvier. The most primitive members of this great group are of course the annelid worms, out of which there arose, some time in the remote past, the primitive Crustacea or trilobites and from this stock not only the later Crustacea but two phyla of air-breathing arthropods. The latter include the more remotely related arachnoids—scorpions, spiders, extinct Merostomata and the relic horseshoe crabs—not all of which, however, are air-breathing. The nearest allies to the insects, on the other hand, are the Myriapoda—millipeds and centipeds, which, while of a lower order of development, show many features in common with the insects.

Definition.—Insects may be defined as air-breathing arthropods in which the body is divided into three distinct regions, the head, thorax, and abdomen. There is a pair of legs borne upon each of the three segments of the thorax, and generally two pairs of wings, arising from segments two and three. The head, which shows no external trace of segmentation, bears a pair of feelers or antennæ, compound and simple eyes, and three pairs of mouth parts—the mandibles and the first and second pair of maxillæ—although the last are more or less united into a single organ, the labium or lower lip. The abdomen, consisting of eight or nine segments, is generally devoid of appendages in the adult. None of the insects are organically united to each other, and but few are sedentary, although many are parasitic in habits and often degenerate. The sexes are entirely separate and the development of the young is often complicated by a more or less profound metamorphosis.

Importance and Numbers.—From the standpoint of their importance, the insects may be placed next to mankind, the only possible disputants being the ungulate mammals, whose significance

is not so much from the viewpoint of nature as from that of man; the insects, however, may be considered important from either point of view.

Their numbers exceed computation, for Kellogg tells us that while there are less than 1000 different bird species in North America, there are more than 10,000 known species of beetles alone, and the total number of named and described species of insects in the world is about 300,000. This is so far, however, from being the ultimate number which the world contains, especially in the teeming tropical forests, that L. O. Howard estimated them at perhaps 3,500,000, and when one multiplies this number by the possible number of individuals of each kind, necessarily variable, he arrives at figures as incomprehensible as the years of geologic time.

Weigh the importance of such an army from the standpoint of its devastation, for it "lives on the country" and every mouth must be filled many, many times! The tax imposed by the insects on mankind alone through their destruction of crops and of raw materials and manufactured products—food, tobacco, drugs, leathers, textiles, buildings—amounts to untold millions of dollars each year. They are the only forms of life which seriously threaten man's earthly supremacy, and while individually their devastations are of little moment, collectively their constant attrition may ultimately effect local conquests in which man will have to confess himself beaten.

In addition to the general destructiveness of insects we have to charge against their general account the direct sufferings of humanity caused by insect-carried diseases, some of which are discussed in the chapter on parasitism, and these sufferings in many instances terminate only in death. But over against this terrible arraignment may be placed to their credit the direct aid of the beneficial insects in the fight against their noxious allies, and the very great service that many of them give in the pollenation and consequent fructifying of the plants, many of which, like the red clover, are important food crops for man or for his beasts. This pollenation has given rise to some intricate adaptations on the part of plants themselves to insure the visits of the fertilizing insects and to enable the pollen to be obtained unconsciously in one flower and left where it will surely impregnate another. To these should be added those insects that are of direct benefit to man, such as the honey-bee, cochineal and lac insects.

Habitat.—The habitat of the insects is as variable as one can conceive of, covering practically the entire range of animal environment with the exception of the deep sea. Among free-living insects there are terrestrial ones, ranging from alpine wastes to the steaming tropical jungles, from the snowfields of the Arctic to the ever green forests beneath the equator, and from the driest deserts to the most humid regions of the world; they range from the air to the waters under the earth, being found even on the ocean many miles from land, some surface dwellers, others subaquatic; and they are miners and borers in wood, and inhabitants of the body of other animals, both within and without, man himself being tenanted by no fewer than a dozen, probably more, different species of insect parasites.

Habits.—Insect habits cover a wider range than those of any other group, and the anatomical structure, especially of locomotive organs and mouth parts, varies astonishingly to suit the owner's habits. It is futile to attempt to mention the habit variation at this place.

Metamorphosis.—The fact that in many insects the growth to maturity is attended by a more or less profound alteration of the creature's form, appearance, and habits, has already been mentioned. In the lowest order, the Aptera or Thysanura, metamorphosis has not yet been acquired, the creature being, at the time of hatching, a miniature replica of its wingless parents. In winged forms, on the other hand, as these useful structures are confined to the adult stage, there is the change from the wingless to the winged condition. Again, in the lower orders where no special type of larva has been evolved to meet peculiar life conditions, the metamorphosis, such as it is, may be said to be incomplete or gradual, for the young are readily recognized as offspring of their parents; and the wings, at first lacking, grow with successive molts until at the last they become functional. Aside from the acquirement of the power of flight, there is therefore no abrupt or decided change in the appearance of the animal. Hence the term larva, which always implies some modification or structure which the adult does not possess, cannot properly be applied to the young of these forms, and they are known as nymphs.

In higher insects, where such larval characters have been acquired, there is no external trace of wings throughout the adolescent life, then comes a remarkable stage interpolated into the life cycle,

during which the insect is generally quiescent and is undergoing its profound change into the form and condition of an adult. In this, the pupa or chrysalis stage, the future external organs—antennæ, wings, legs—may be externally manifest, reminding one of an Egyptian mummy case upon which are moulded and painted the features and something of the form of its silent occupant. The emergence from the pupa skin is almost like a resurrection, for the creature now comes forth glorified and resplendent to wing its way through the air, whereas before it was a creeping, earth-borne form. The several stages are:

Egg	Adolescent	Adult
Where metamorphosis is gradual		
Egg	Nymph	Imago
Where metamorphosis is complete		
Egg	Larva Pupa	Imago

Flight is *never* acquired in existing insects before the imago state is reached, when the individual, whatever its size, is full grown and after which it ceases to molt. The only apparent exception to this rule is in the May-flies (Ephemerida) in which the creature emerges from its aquatic home, molts, spreads some very imperfect wings, flies to the nearest support and molts again, this time developing perfect wings with full powers of flight. This temporary flying condition is known as the subimago stage, and is really comparable to the last nymphal stage in other insects wherein the wings are present and rather large but not yet functional.

Classification.—A brief résumé of insect classification is necessary to our further study, but while specialists would divide the group into more than twenty orders, a more general grouping into nine will serve our purpose.

A. *With no metamorphosis*

Order 1. **Thysanura** or **Aptera.**—Wingless insects with the body covered with scales or hairs. Eyes either absent, simple in groups, or compound. Some run, others progress by means of a springing apparatus on the abdomen. Examples: the springtails (*Podura*) and silverfish (*Lepisma*).

B. *With incomplete metamorphosis*

Order 2. **Orthoptera.** Insects with two pairs of wings of which the anterior pair are generally parchment-like (tegmina), the posterior ones

membranous. Mouth mandibulate, that is, with the normal insect jaws, fitted for chewing. This order includes the earwigs, cockroaches, stick and leaf insects, grasshoppers, and locusts.

Order 3. **Pseudoneuroptera.** Insects with two pairs of similar, net-veined, membranous wings. Mouth mandibulate. Includes the termites or "white ants," May-flies, dragon-flies, etc.

Order 4. **Hemiptera.** Insects in which the wings are usually present and are sometimes similar and membranous, again dissimilar, the forward pair having thickened bases and membranous extremities which overlap (hemelytra). Mouth haustellate, *i. e.*, sucking, consisting of a rostrum enclosing the jaws, which are modified as piercing organs. This order includes the bugs, lice, scale insects, plant-lice or aphids, and cicadas.

C. *With complete metamorphosis*

Order 5. **Neuroptera.** Similar to the Pseudoneuroptera, except that the metamorphosis is complete. Formerly included that order under the present name. Examples: ant-lions, aphis-lions, and caddice-flies.

Order 6. **Lepidoptera.** With two pairs of well-developed wings which are covered with scales. Mouth haustellate as adult, mandibulate as larvæ. Butterflies and moths.

Order 7. **Coleoptera.** Insects with dissimilar wings, the anterior pair being in the form of horny elytra, the posterior pair membranous. Mouth mandibulate. Beetles.

Order 8. **Diptera.** Winged or wingless (fleas) insects, the former having but a single pair of membranous wings, the hinder ones being represented by a pair of knobbed balancers or halteres. Mouth haustellate. Here are included the flies, fleas, and certain degraded, tick-like, wingless flies.

Order 9. **Hymenoptera.** Insects which generally possess two pairs of similar and membranous wings. Mouth mandibulate or haustellate (licking). Includes the bees, wasps, ants, gall- and ichneumon-(parasitic) flies.

Adaptive Radiation of Insects

The law of adaptive radiation (see Chapter XVIII), which was originally applied to the mammals, is equally applicable to the reptiles on the one hand and to the insects on the other. There is, however, this difference in the insects, that while the primitive stock was undoubtedly terrestrial, as in the two vertebrate groups, most insects have passed through a volant or aërial stage. This volant stage, while it has also developed both in mammals and in reptiles, is confined to relatively few forms, none of which, once having attained it, has ever retrogressed. The insects above the Aptera, therefore, are in a sense more comparable to the birds in that practically all fly, and those which do not, come from a volant ancestry and have lost their wings through specialization.

On the other hand, the birds are hardly comparable to insects in the extent or range of their adaptation.

DIAGRAM SHOWING ADAPTIVE RADIATION OF INSECTS

Cursorial
Roaches
Ground beetles

Volant
All but Aptera, especially dragon-flies, bees, wasps

Primitive stock
Aptera

Aquatic
Beetles and bugs
Many nymphs of Pseudoneuroptera and young of Diptera

Fossorial
Many larvæ of beetles and cicadas, but especially mole crickets

Primitive Stock.—The simplest living insects are undoubtedly the Aptera (Thysanura), for here alone we have primarily flightless forms, shown not only by the total absence of wings within the order, but also by the simplicity of the thorax and its musculature as compared with secondarily flightless forms, since here we find the three segments of the thorax separate and not fused (Fig. 113). These forms are not known fossil before Carboniferous time (*Dasypeltus*), but there has been little change from that day until the present, and this argues for their high antiquity. In the more generalized flying insects the first segment or prothorax alone is free, whereas in the higher forms—Hymenoptera, Lepidoptera, Diptera—all three segments are united into a firm box wherein the wonderful motor organs reach their highest development.

FIG. 113.—Fish-moth, *Lepisma* sp. (From J. B. Smith's *Economic Entomology*.)

Cursorial and Saltatorial Adaptation.—Cursorial forms are represented by the cockroaches

among ancient types, and although many of their allies to-day have departed from the more primitive cursorial gait and have become leaping or saltatorial forms, as in the grasshoppers and crickets, speed of movement is characteristic of both. Among the Orthoptera the cursorial gait was prevalent during the Paleozoic, leaping forms being unknown before Lower Jurassic (Lias) time. Among the ancient cursores more than two hundred species of roaches have been described from the Paleozoic, some of them of gigantic size.

Certain beetles, notably the ground beetles, Carabidæ, and the tiger beetles or Cicindelidæ, are cursorial. The latter especially are the most agile of all beetles and are not only swift of foot, but are also able to fly well. They are gracefully formed and beautifully colored and, as one would expect, are predaceous forms of high economic value through their destruction of noxious insects. The ground beetles are a large group almost all of which are predaceous in habits, either springing upon their prey or capturing them by chase.

Many of the Hymenoptera are also speedy, especially the true ants and the so-called velvet-ants (Mutillidæ) which are in reality wasps. Here the male flies, but the female is wingless, very swift in her movements, a powerful stinger, and warningly colored in scarlet and black. The true ants which, with the exception of the sexed individuals, have also lost the power of flight, make up for it by the rapidity of their movements. Speed adaptation is shown in all of these forms by the graceful bodies and slender limbs, in sharp contrast to certain of their non-cursorial allies, such, for instance, as the heavy-bodied boring and scaraboid beetles, and the bumblebees.

FIG. 114. — Fossorial mole-cricket, *Gryllotalpa borealis*. (After Comstock.)

Fossorial Adaptation.—Fossorial insects are many, some digging for retreat as in many wasps and bees, others merely for nest-building to provide safe asylum for the eggs and helpless young. Others, like the larvæ of the leaf-chafers (June bug, Japanese and May beetles, etc.), are entirely subterranean and as "white grubs" take a substantial underground toll of the farmers' crops.

The fossorial insect *par excellence*, however, is the mole-cricket (*Gryllotalpa*) which in its habits and appearance simulates quite closely the common garden mole. The body, while long and rather slender for a cricket, is on the whole spindle-shaped, the small head forming a good entering angle, offering but little obstruction to passage through the soil. The fore limbs in particular are mole-like, broadened, the tibiæ being expanded and spined in such a way as to be most effective digging organs. In their broad sidewise sweep they resemble the mole's hands in action, and, like the mole, the cricket's movements can be detected as he progresses just beneath the surface (see Fig. 114).

Aquatic Adaptation.—There are many different adaptations to aquatic life among insects, some of which apply only to the adolescent life, others to the entire insect career, and the adaptations include not only locomotor devices, but special respiratory structures whereby what are primarily air-breathing forms have become able to utilize the air dissolved in the water. These structures, as we shall see, are of greater significance than their present use implies, for it is believed that out of such structures the insect wing evolved (see page 416).

The aquatic groups may be summarized as in the table on the following page (adapted from Comstock):

	Adolescent	Adult
Pseudoneuroptera		
Ephemerida, May-flies	Aquatic	Aërial
Odonata, dragon-flies	"	"
Plecoptera, stone-flies	"	"
Hemiptera		
Corisidæ, water boatmen	"	Aquatic
Notonectidæ, back-swimmers	"	"
Nepidæ, water scorpions	"	"
Belostomidæ, giant water bugs	"	"
Naucoridæ, creeping water bugs	"	"
Veliidæ, water striders	"	"
Hydrobatidæ, water striders	"	"
Neuroptera		
Sialidæ, dobson, etc.	"	Aërial
Phryganeidæ, caddice-flies	"	"
Coleoptera		
Haliplidæ, haliplids	"	Aquatic
Dytiscidæ, predaceous diving beetles	"	"
Gyrinidæ, whirligig beetles	"	"
Hydrophilidæ, water scavengers	"	"
Diptera		
Blepharoceridæ, net-winged midges	"	Aërial
Culicidæ, mosquitoes	"	"
Simuliidæ, black flies	"	"
Ephydrinæ	In marine or alkaline waters	"

In the more generalized insects whose young are aquatic, this adaptation may perhaps be looked upon as a primitive condition; among the flies, on the other hand, it may well be a secondary adaptation. There is apparently no insect that is aquatic as an adult only.

Of the *aquatic modifications*, the first to be considered is the means of respiration. As we have seen, the respiratory organs of the spiders, myriapods, and insects consist of branching air tubes known as tracheæ which have their origin in symmetrically arranged apertures, the stigmata, through which free air is admitted to the system. There are generally a pair of principal longitudinal trunks from which short tubes pass to the stigmata. From them there also arise other branches (see Fig. 12) which divide and divide again until they end in tubes of capillary fineness which are found in all of the tissues of the body.

Usually among animals the blood or its equivalent is the oxygen-carrying medium, receiving it from the respiratory organs (external

respiration) and delivering it to the tissues (internal respiration), the oxygen being carried in chemical union with an iron compound, hæmoglobin, in which case the blood is red, or with a compound of copper, hæmocyanin, which gives a faint bluish tinge or none at all to the blood. With the tracheates the blood has no respiratory function, the air being carried bodily wherever it is needed by the tracheal tubes which, in common with other respiratory devices, are merely a complicated infolding of the body-wall.

Aquatic insects breathe by one of two general means, either by air reservoirs or by tracheal gills. In certain insects which, like the water bugs or water beetles, are aquatic throughout their life, the abdomen is flattened on its dorsal surface, but the forward wings are arched in such a way that a space of considerable size is left into which the tracheæ open. The insect, which requires but little air compared with a vertebrate, comes to the surface from time to time, protrudes the end of its abdomen, raises the wing tips slightly, and thus renews the air in its reservoir. But the young of these same insects have no wings, so another method must be adopted to take the place of the reservoir, and this is done by having the body clothed with hair in which aîr becomes entangled, being separated from the surrounding water by the so-called capillary film in the form of an air bubble. From time to time the insect can come to the surface and renew the air, but in well aërated water this is not so necessary as with the winged form, for oxygen passes inward and carbonic acid gas outward through the capillary film by osmosis, that process by which gases or other substances on either side of a film or membrane are equalized.

Tracheal gills (see Fig. 115) are leaf- or hair-like outward extensions of the body-wall, arising from a stigma, the tracheæ being continued into them and branching out like the veins of a leaf. The air within is now in osmotic relationship with the surrounding water which bathes the gill, and as before the mutual exchange of gases is effected. Respiratory movements keep up an interchange of air from the gills to the bodily tracheæ and by the rhythmic waving of the former or by motions of the insect's body the water immediately surrounding the gill is renewed. In the May-fly nymphs the gills are arranged in pairs along the sides of the abdomen, a pair to each of the several stigmata; in the stone-flies they lie, as they rarely do, on the sides of the thorax at the base of the limbs. In the smaller dragon-flies, Agrioninæ, the gills are leaf-like

expansions borne at the end of the body. These subserve not only their prime function of respiration but, as with a caudal fin, the secondary one of locomotion as well. The larger dragon-flies, Libellulinæ, differ in not having external gills, but an internal one, in that the rectum, the posterior portion of the alimentary canal, with its walls filled with tracheæ, functions as such. Here rhythmic contraction and relaxation of the muscles causes a tidal ebb and flow of water through the anal aperture, bringing the fresh supply of oxygen and removing the effete material. Incidentally this structure also becomes a locomotor organ, for the forcible expulsion of the water from the rectum drives the creatures forward by a method of jet-propulsion comparable to that seen in the squid.

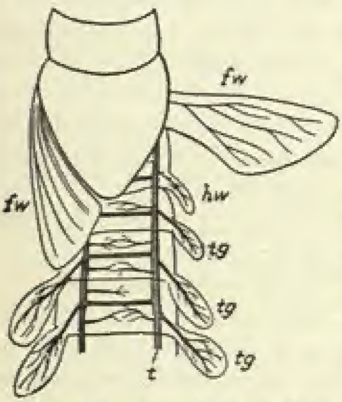

FIG. 115.—May-fly larva, showing tracheal gills. *fw*, fore wing; *hw*, hind wing; *tg*, tracheal gill; *t*, tracheal tubes. (After Lang, from Parker and Haswell.)

The combination of respiratory and locomotive function in the tracheal gill is significant, as these structures, especially such as are seen in the May-fly nymphs, are thought to represent the prototype of the insect wing (see page 417).

Aside from the breathing devices, the body and limbs also show aquatic modifications, especially when the creature is nektonic. In a bottom-clinging form no special aquatic adaptation is necessary, but the predaceous diving beetles and the back-swimmers and water boatmen among the bugs show more or less physical conformity to the needs of the environment, with stream-line bodies which bear no unnecessary projections. They do not, perhaps, follow the numerical lines to the extent that the fishes do, but sufficiently so for small, not over-swift craft. The limbs often show oar-like expansions whose extent is sometimes increased by lateral fringes of hair; propulsion, if not by tracheal gills or the rectum, is invariably by means of the limbs and, as among aquatic reptiles and mammals when this is the case, the rate of speed is necessarily limited. Perhaps the larger dragon-fly nymphs which sweep the limbs backward simultaneously with the drive of the rectal jet

are among the most rapid insect swimmers for a short distance. Add to this a remarkable extensile labium for grasping their prey and their efficiency is as great in its way as that of the magnificent adult. The nymphs are generally protectively colored so that their quick dart from obscurity must make them highly successful in the struggle for existence. Among the most interesting of aquatic insects are the caddice-worms, larvæ of the caddice-flies and belonging to the true Neuroptera, yet probably ancestrally related to the butterflies and moths as well. The adult is a small nocturnal insect, of somber hue, looking when at rest not unlike a night-flying moth. The wings are clothed with hairs, not scales as in the Lepidoptera, but these scales are in turn modified hairs, which among other things makes the above-mentioned relationship plausible. The larvæ are caterpillar-like, the elongated abdomen being decked with tufts of hair-like tracheal gills. Instead of exposing its tender body to the vicissitudes of aquatic life the creature makes for itself a tubular house within which it lives and from which its head and limbed thorax may be protruded for locomotive purposes. These houses vary in building material as well as in architectural design, being formed of tiny bits of twigs or leaves, or of sand grains or even minute pebbles, the twigs sometimes laid lengthwise, again after the manner of a pioneer's log cabin. The creatures themselves are carnivorous and occasionally spin a web athwart the current of the stream, like a tiny fisherman's net, and lie in wait as a spider does for such unfortunates as chance provides for food.

FIG. 116. — Water beetle, *Hydrophilus triangularis*. (After Bruner, from J. B. Smith's, *Economic Entomology*.)

Aërial adaptation is so universal an insect characteristic that but few forms need be mentioned as of particular interest in this regard The powers of flight among insects vary astonishingly. Some are slow, bungling fliers, as certain of the Lepidoptera or flies; others, like the larger dragon-flies, are tirelessly on the wing and the rapidity of their movement has given them a number of colloquial names, such as arrows, devil's darning needles, snake doctors, and spindles, and this and their general conspicuousness have given them a wholly undeserved disrepute. Certain flies are also im-

mensely speedy, their compact thorax, powerful musculature and single pair of very efficient wings serving to drive them at a rate which, in proportion to their size, is truly remarkable. Thus the horse-fly is able to outstrip the swiftest horse. The rate of vibration of the common house-fly's wings, which produce approximately the sound of F, has been computed to be about 21,000 times a minute or 335 times a second, and these figures have been confirmed graphically by Marey, who found that the fly actually makes 330 wing strokes a second (Packard).

The *wings* of insects are never homologous with those of the several vertebrates which have attained flight, the pterosaurs, birds, and bats, for here the wing is always a modified fore limb, whereas in the insect it is merely an expanded and highly modified portion of the body-wall (see Fig. 12). The wings of the ancient insects such as the Paleozoic cockroaches were more horny and that is still true of the fore wings of the lowlier orders, Orthoptera, Hemiptera, and Coleoptera. Secondarily they became membranous, and finally, the complex organ in its venation and embellishment that we find in the higher types. Insects' wings also differ from those of the vertebrate in their flatness, for the upper and lower surface, with the exception of the beetles' horny fore wings or elytra, are practically the same, whereas in the bird especially the upper surface is convex and the lower one concave. The motion described by the wing also differs, for that of the insect moves in a figure 8, while the bird's motion is simpler. This may be due to the form of the wing which when vibrated bends in such a way as to describe that curve, or may be due to the method of articulation of the wing with the body. In many heavier insects like the beetle the creature is like a biplane, the wings being quite separate, and in some instances the elytra are not vibrated at all but are merely supporting planes, the hinder membranous wings constituting the motive power. Again, as in the bees, the fore and hind wings are articulated together by a series of hooks so that they move as one. It is notable that among the swiftest insects, the flies, the creatures are monoplanes, which is equally true of man-made flying machines.

The origin of flight in insects is not surely known. Gegenbaur would derive the wings from the leaf-like tracheal gills of which we have spoken. There is, however, no insect known in which such a gill may be seen in a transitional state of development into a wing, and between the largest

and most efficient gill and the smallest structure which could possibly support the creature in flight there is a material gap. Some intermediate function between respiration and flight seems necessary. We can imagine an overlapping of functions, but it is difficult to conceive of the progressive development of a temporarily useless organ, unless by the unproved theory of orthogenesis or the occurrence of brusque mutations to close the gap.

Another theory of origin of wings, however, seems to bear the confirmation of paleontology. In Carboniferous and some Permian insects all three thoracic segments are more or less alike and the prothorax does not show the various degrees of specialization seen in later forms. But what is even more significant is the presence of lateral outgrowths on the first thoracic segment which resemble small wings (see Fig. 120,A). So many unrelated Paleozoic groups display these wing-flaps that it seems likely that such structures were present in the ancestors of all flying insects. In all probability similar flaps were present on all three segments and for some reason only those of the second and third segments developed into functional wings while those of the first, after persisting for a while, gradually disappeared as aborted structures. Certain modern insects show a similar tendency; diminishing the second pair of wings which in their ancestors were nearly or quite equal in size to the first pair. This is true of the May-flies, the dragon-flies, and those of the Hymenoptera in which the reduced hind wings are articulated to the fore wings so that both act as one. The tendency culminates in the true flies or Diptera in which mere vestiges of the hind wings remain. This does not in the least impair the function of flight, for the flies are among the swiftest of insects. An analogy with the development of the airplane may be seen, for both the insect and machine were at first biplanes, the function of support being assumed by a single surface, until the condition of a monoplane has been reached. But here the analogy ceases, for in the insect the functions of support and propulsion are combined in the same organs but are separated in the plane.

The development of flight among insects implies therefore, first, a departure from the old terrestrial habitat into the water. If this were done by a small insect, which was probably the case, the only adjustment necessary would be a reduction in the thickness and firmness of the cuticle so that the entire body might subserve the respiratory function. The insect was doubtless one of those living in damp situations, such as the present-day Thysanura (Aptera). These forms have retained the ancient habitat and probably have persisted with little change from remote geologic time. With increase in size and consequent muscular development, however, came a thickening of the cuticle and a consequent localization of the respiratory function. Gills arose through a necessary increase of respiratory surface, resulting in outpushings of the thinner por-

tions of the body-wall. These, which may be called blood gills, served to aërate the blood directly through their surface. Their subsequent invasion by tracheæ followed, so that the blood merely acted as an intermediary between the tracheal air and that in the surrounding water, and finally the tracheal gill was perfected. Next came the differentiation of the gill into a respiratory and a protective part, the latter becoming movably articulated with the body to aid in renewing the water over the respiratory gill. The subsequent enlargement of the gill-cover to embrace several gills, the suppression of the latter when, at the last molt, the creature reëmerged on land as an adult, the use of gill-covers as imperfect wings, and their final perfection as organs of flight complete the process. This implies of course a single evolution of flight on the part of a primitive insect out of which all of the orders, except the Aptera, have subsequently arisen.

Other theories of wing origin have been proposed, such as lateral expansions of the dorsal wall of the thorax, which served first as airplanes for a leaping form, and subsequently became hinged and muscled; but the theory of the tracheal gill origin seems to have the weight of evidence in its favor.

Geological History

Ancestral Stock.—Handlirsch has demonstrated the primitive character of the trilobites (see Fig. 117), Paleozoic arthropods the true position of which was long in doubt and which he holds to have been the original stock out of which arose as independent phyla the various arthropodan classes. Out of the trilobites the Crustacea were first differentiated, and from this line arose, in the course of time, all of the gill-breathing shrimp- and crab-like forms, together with hosts of lesser allied creatures whose descendants teem in the fresh and salt waters of to-day.

Of the arachnoids, the scorpions also arose from the trilobites through an intermediate eurypteroid ancestry, of which a lone survivor, *Limulus*, yet lives—the only living gill-breathing representative of the class. The ancient eurypterids of the Ordovician and Silurian (see Chapter XXVIII) were also related to the limuloids, but like the vast majority of the latter they have entirely ceased to be. Scorpions are especially noteworthy, for specimens of *Palæophonus* found in the Silurian rocks of Scotland and England, and *Proscorpius* from the Silurian of

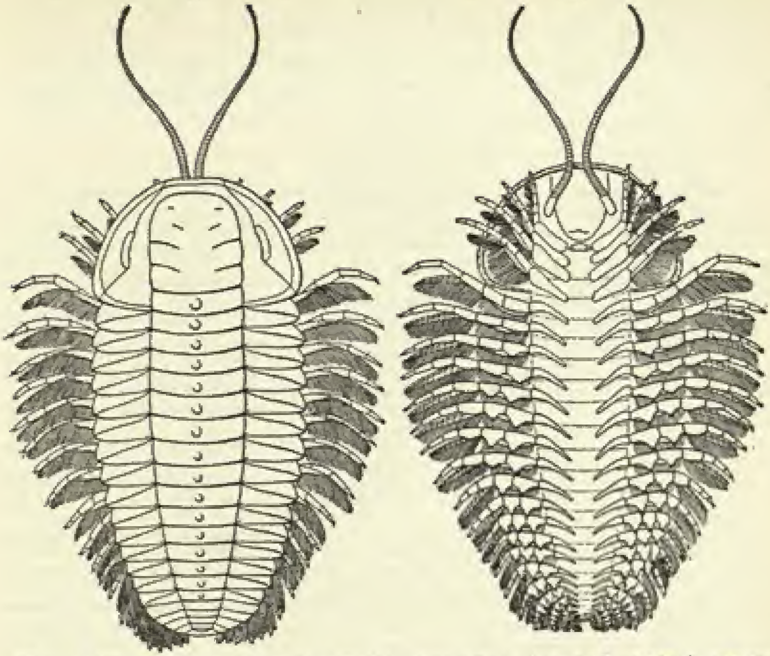

FIG. 117.—Trilobite, *Triarthrus becki*, restored. 1, dorsal, 2, ventral aspect. Twice natural size. (After Beecher.)

New York are the first recorded relics of air-breathing animals (see Fig. 118).

The myriapods are seemingly difficult of derivation from the trilobites and yet there are certain Carboniferous myriapod-like forms which suggest relationships between the two groups even here.

Handlirsch would derive winged insects directly out of the trilobites, setting aside the primitive Aptera as degenerate forms. There seem to be many difficulties, however, in the way of this assumption, even with the Aptera as an intermediate stage. G. C. Crampton, although using but a single structure, the mandible, by way of evidence, proves, nevertheless, that a great many intervening stages must have existed between the rather complex structure in the trilobite and its simple homologue in the insect. His hypothetical ancestor stock is therefore truly crustacean, "anatomically intermediate between the Mysidacea on the one side and the Syncarida on the other. . . . Starting from this common source,

the lines of descent of the Insecta were paralleled on one side by the 'higher' Crustacea and on the other by the lines of descent of the Symphylo-Pauropoda" (myriapods). He further concludes that the Crustacea not only approach closely to the insectan type, but that they also furnish us with a long series of intermediate stages connecting the insect types of structure with the lower arthropods, such as the trilobites.

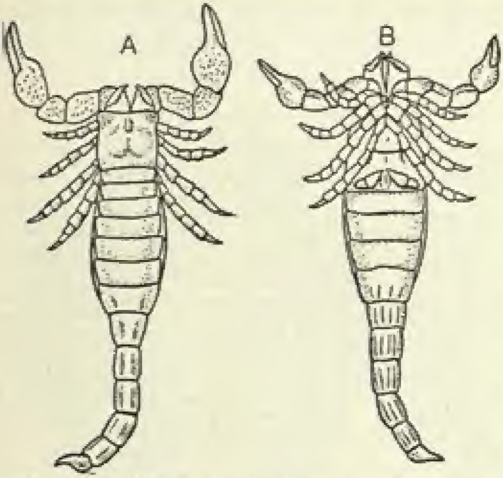

FIG. 118.—Silurian scorpions, restored. A, *Palæophonus nuncius*, dorsal aspect; B, *P. hunteri*, ventral view. (After Pocock, from Schuchert's *Historical Geology*.)

Primal Insects.—The Palæodictyoptera were the most primitive winged insects. These appear first in the Carboniferous and are thus described: Insects of primitive organization, with a relatively small head bearing masticating mouth parts. The three thoracic segments were similar, the second and third bearing nearly equivalent wings, the venation of which was primitive. These wings were apparently incapable of being folded backward over the abdomen, their motion being limited to the vertical plane. In addition to these wings, another pair, rudimentary in character, were sometimes borne on the first thoracic segment. The abdomen consisted of ten similar segments which often bore lateral lobes, sometimes serving as tracheal gills (see page 414), in addition to which a pair of long cerci were borne on the terminal segment (see Fig. 120). The legs, of which there were the normal insect number of six, were similar and adapted for walking.

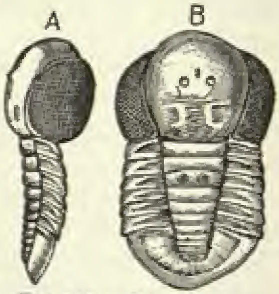

FIG. 119.—Primitive trilobite, *Æglina prisca*, Ordovician, Bohemia. A, right side; B, dorsal view. Enlarged. (After Barrande, from Eastman-Zittel.)

These archaic insects were probably all carnivorous, their young being aquatic in habit and developing into the adult state without a complete metamorphosis, that is, without a quiescent pupa stage (see page 407).

Transitional Orders.—The Carboniferous saw the rise and passing of this group and also the origin from certain of its members of the varied transitional types which were in turn to evolve into the modern orders. These were also comprehensive or synthetic types, combining in certain instances the characteristics of the several orders to which they eventually gave rise. Such, for instance, were the Protodonata, intermediate between the Palæodictyoptera and the Orthoptera or dragon-flies, the Protephemerida, leading to the Ephemerida or May-flies; the Protorthoptera, ancestral to the Orthoptera, the grasshoppers, crickets and the related phasmids, earwigs and the like. Another of these transitional groups was the Protoblattoidea, primitive roach-like forms ancestral to the cockroaches (see Fig. 121), termites, book-lice, bird-lice, and beetles. The other familiar orders such as the Hemiptera or bugs, the Hymenoptera or bees and ants, the Lepidoptera or moths and butterflies, and the Diptera or flies, are of later origin, although from the same Carboniferous Palæodictyopteran stock.

FIG. 120.—Paleozoic insects. A, *Stenodictya lobata*, and B, *Eubleptus danielsi*, primal winged insects or Palæodictyoptera. (After Handlirsch.)

All of the Paleozoic insects were large, and this was especially true of those of the Carboniferous, for a cockroach of the Middle

Carboniferous was as long as one's finger, while certain dragonflies attained a wing-spread of 29 inches. Large size usually accompanies lack of other specialization, and so it was with these creatures, all of which were of relatively simple carnivorous habits, with adaptations showing as yet none of the intricate detail which characterizes the insects of to-day. All were voiceless, none had special larva or pupa forms, but in the fern-like venation of the wings of the roaches, for instance, the first tendency toward protective mimicry is seen.

All plant nature at this time was monotonous and the insects reflect the aspect of the period. Not all, however, were amphibious, for in certain of the transitional orders, Protorthoptera, Protoblattoidea, etc., the ancestral waters had already been forsaken even by the young. Thus the insects parallel the emergence and evolution of the contemporary vertebrates, the amphibians and reptiles (see Chapter XXIX).

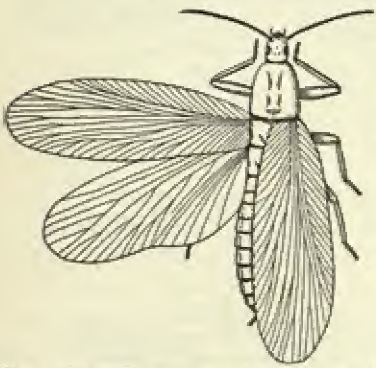

Fig. 121.—*Eucænus ovalis*, ancestral cockroach. (After Handlirsch.)

During Carboniferous time, the climate was mild and humid, with no dry seasons nor cold winters to cause periodical cessation of insect development. This climatic condition is attested by the fact that none of the trees of this time show annual rings of growth. Hence the insect activity was continuous and no adaptations to withstand periods of inclemency were necessary. With the Permian, however, came aridity of increasing severity, and glacial conditions of an austerity even greater than that of the Glacial period of the Pleistocene. This meant a profound alteration of the face of nature, not only of the plants but of the animals as well. Its influence on the vertebrates will be discussed later (see Epilogue), but its effect on the insects was also profound in that it meant a large destruction of such of the primitive forms as were not adaptable, and the modification of such as were. It was probably only in the more favored localities that even such survivals could occur.

Mesozoic Insects.—During the Permian and Lower Triassic, insects were relatively rare, as their great scarcity in the deposits

of those times would imply. When they again appeared the old transitional groups had given way to the modern orders, many of which had acquired the complete metamorphosis with an adaptive resting or pupal stage. This stage may well have arisen as a response to periodic inclemency, but it made possible the profound reorganization which the insects of complete metamorphosis undergo, and the consequent remarkable adaptations of so many of the modern adults. Thus it was in the Trias that the first insects with complete metamorphoses appeared, including the first true beetles, some of which forsook the universal carnivorous habits of their Paleozoic ancestry and fed upon wood.

In the Lias or lowermost Jurassic, the remains of fossil insects again become abundant, many of them reminding one strongly of modern forms and showing in some instances adaptation to a plant diet. In the Middle Jurassic (Dogger) occur the first Lepidoptera and in the Malm (Upper Jurassic) the first Hymenoptera. These were probably plant-feeders, but owing to the absence of flowers none could have had the honey-feeding habits of their descendants.

Higher Orders.—The Cretaceous, however, saw the great development of the dicotyledon flora which before its close had become essentially modernized, so much so that the trees and flowers would probably have had a very familiar look even to our modern eyes. This change had a wonderful effect upon the insect hosts, for flower-feeding forms were now possible and through mutual interdependence the insects must in turn have stimulated the rapid evolution of floral adaptation.

Tertiary Insects.—With the coming of the Tertiary the entomological aspect of nature again changes and there appear all of the higher orders in contrast with those of the Lias. Now for the first time occur the social insects—termites, ants, bees, and wasps—as well as the insect parasites of warm-blooded animals. The development of insects during and since the Tertiary has been along the lines of marvellous increase in the number of species, high specialization, small size, parasitism, and communal life.

Summary.—Three great events of geologic history stand out as the impelling forces of insect evolution. The primal cause for the origin of insects from their trilobite ancestry was the great development of the land flora and fauna in the Silurian and more especially in the Devonian. The Paleozoic insects of primitive or

transitional types thus arose and flourished but with conservativeness, except for size, until the second profound event occurred.

This second cause was the great climatic change in the Permian, which eliminated so many of the archaic forms and introduced a new condition, that of complete metamorphosis with its attendant chain of possibilities, into many of such as survived.

The appearance of flowering plants in the Cretaceous completed the work and there were consequently evolved into being the higher orders which are so largely dependent upon flowers or flowering plants, either directly or indirectly, for their sustenance. Thus, as Handlirsch says: "Through the study of the paleontology of insects we again see clearly how great was the influence of the changes in the outer living conditions on the origin of new forms, and we see further that the environmental conditions led ofttimes to a remarkably rapid differentiation."

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CHAPTER XXVIII

ORIGIN OF VERTEBRATES

We have in the two preceding chapters discussed the evolution of two of the three great lines of descent which the animal kingdom includes. The third line, that of the vertebrates, is to be the subject of our research from now on, to enable us to comprehend in full the place in nature held by mankind.

Definition of a Vertebrate

Notochord.—Vertebrates, or to use the more comprehensive term, chordates, have several diagnostic characters which are absolutely distinctive, separating them sharply from all other forms of life. Of these, the first is the possession of a notochord (Gr. νῶτος, back, and χορδή, cord). This is an internal axial stiffening running lengthwise of the trunk and serving to resist the bodily shortening which the contraction of the muscles would otherwise cause. In its most primitive form the notochord is membranous, composed of cellular connective tissue, the cavities of which are so distended with fluid as to render the whole structure turgid, resistant to pressure, but highly elastic. Later the notochord becomes cartilaginous, to be replaced in higher forms by the bony vertebral column consisting of a number of short but often complex vertebræ separated, for mobility, by cartilaginous intervertebral discs.

Perforated Pharynx.—The development of apertures known as gill-slits through the walls of the pharynx or throat cavity is the second chordate character. These vary in number from a pair to more than a hundred (*Amphioxus*) and are always present, but by no means always retain their ancient respiratory function, for with ourselves and other mammals, the slits, of which there are several pairs in the embryo, are reduced in number until but one pair is left and these form the eustachian tubes which serve to equalize the air pressure on either side of the ear drum by connecting the middle ear with the cavity of the throat.

Neurocœle.—The third diagnostic character is a hollow nerve cord, the so-called spinal cord, which lies immediately above the

notochord or the vertebral column. This may be a very simple structure, or again its anterior portion may increase and develop until in its highest expression, the human brain, it has formed what is probably the most intricate thing in nature. In every case, however simple or complex it may be, the internal canal or neurocœle persists, though exceptions may be said to exist in the tunicates or sea-squirts, which are striking examples of degeneracy resulting from sedentary life (see page 434). In them the active larva has a nervous system which conforms to our definition, but

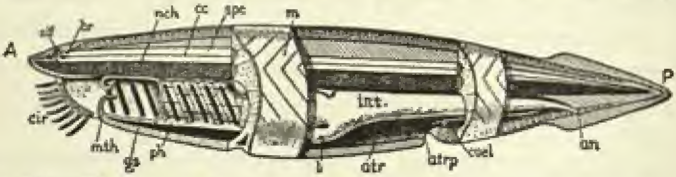

FIG. 122.—Diagram of *Amphioxus*. A, anterior end, P, posterior end. *an*, anus; *atr*, atrium; *atrp*, atriopore; *br*, brain; *cc*, central canal (neurocœle); *cir*, cirri; *cœl*, cœlome or body cavity; *gs*, gill slits; *int*, intestine; *l*, liver; *m*, muscle bands (myomeres); *mth*, mouth; *nch*, notochord; *olf*, olfactory pit; *ph*, pharynx, *spc*, spinal cord. (After Parker and Haswell.)

in the adult it is reduced to a single ganglion, or mass of nerve matter, with no trace of the neurocœle.

Other Characters.—Other distinctive features are usually shown by chordates. They are generally segmented, the segmentation showing in the nervous system, gill-slits, vertebral column, ribs and breast-bone, and in the muscles of the trunk. When paired limbs are present, their number never exceeds four, while in the invertebrate there is no such limitation. Finally, there is apparently a reversal of surfaces, for whereas in the invertebrate the bulk of the nervous system lies *below* the gut and the blood system *above*, in the chordate the reverse is true. In the invertebrate the body-wall is equally thick throughout, in the vertebrate there is a remarkable thickening or concentration of the muscles along the dorsal side within which lie the notochord and spinal cord.

It is, therefore, this group of forms, comprising the degenerate tunicates, the unprogressive *Amphioxus*, the fishes, amphibians, reptiles, birds, mammals, the last of course including man, that we wish to consider, and our immediate problem is to learn, if possible, the time, place, and source of vertebrate beginnings.

Time of Origin

The chordates are a very ancient race, dating back probably to the beginning of Paleozoic time, although the tangible record of their existence commences with the fragmentary remains of armored "fishes" (ostracoderms) found in Middle Ordovician rocks near Canyon City, Colorado, in the Big Horn Mountains of Wyoming, and in the Black Hills of South Dakota. But these relics are those of creatures which had already traveled far along the evolutionary road and, according to most authorities, do not represent the most primitive members of the chordate stem. Hence we may safely say that the time of origin was not later than the beginning of the Ordovician, and probably long before. There is, however, little chance of finding the geologic record of the ancestral forms, if, as we may suppose, they were soft-bodied, delicate organisms without hard parts for fossilization. An apparent exception lies in the little "fish plate," *Eoichthys howelli*, discovered in the Cambrian shales of St. Albans, Vermont, in 1926. Later study shows this fragment to have been misinterpreted, so the Ordovician record still stands.

Place of Origin

The main contrast between invertebrate and vertebrate animals seems to be that, as a whole, the former are static organisms with little or no power of locomotion, while the latter are essentially dynamic. There are of course exceptions in each group, for the cephalopod molluscs, squid, etc., are splendid locomotor types, and some chordates have become sluggish or even fixed as an outcome of sedentary habits. Whether or not this contrast of type is a result of the physical environment, invertebrates to static marine waters and the vertebrates to dynamic fresh-water streams, as Chamberlin held, is not at all clear. The most primitive chordates existing to-day—tunicates, *Amphioxus*, etc.—are marine, inhabiting for the most part the flatsea (see page 55), where they lead a wholly or partially sedentary life.

That this is therefore the ancestral habitat seems at first sight plausible, yet within this area there seems to be lacking the necessary physical or external stimulus to impel the evolution of the chordate characteristics, especially segmented body muscles and the notochord. Perhaps the strongest stimuli would be escape and pursuit and the need to remain in the environment. The cepha-

lopod locomotion, acquired in the sea, is largely for the former purposes and is based on an entirely different principle from that of the chordate. There are, however, among the segmented worms, marine forms which swim by a wriggling or undulatory movement comparable to that of the vertebrates, except that it is up and down or dorso-ventral, instead of from side to side or lateral. There is no reason, however, why the sea might not have produced the one as well as the other. Briefly, Chamberlin invoked the dynamic rivers which would give the undulatory movement, extrinsically, to a passive elongated animal temporarily anchored by the mouth. He imagined that the creature might learn to produce the same movements actively, in order to avoid being swept out of the environment into the sea, and thus develop motor organs accordingly, an idea which has had very little general acceptance. Frankly, we do not know the place of origin, nor is there any direct evidence which can be brought to bear upon the problem.

Ancestral Stocks

Several theories have been advanced to set forth the claim of this or that invertebrate group to vertebrate ancestry, but none of them is at this time capable of adequate demonstration. Of these, three are based upon the assumption that a segmented ancestry is necessary to account for the segmentation seen in the vertebrate, an inference which is not necessarily true, as segmentation may readily have arisen anew in the chordate phylum as a response to such conditions as those postulated by Chamberlin.

Annelid Ancestry.—The hypothesis of annelid ancestry for the vertebrates derives the primitive chordate from the phylum Annelida, typified by the earth- and marine-worms. In many of the principal organs there is a marked correspondence, with the exception of the general reversal of the relations of the various parts to one another. For, as we have seen, the relative position of blood and nervous systems is diametrically opposite in the vertebrate and invertebrate groups. But by postulating a physiological reversal of the animal—and we know that in the flounder and squid such a change from the morphologically normal posture can take place—the various organs of the worm may be brought into almost complete harmony with those of the vertebrate. Perhaps the greatest difficulty lies in the development of the notochord, but even this seems to have its annelid prototype in "the 'Faserstrang,' a

bundle of fibers running along the nerve chain and serving as a support. This and the notochord lie in a precisely similar position in relation to the other organs, and in both cases they are enclosed with the nerve cord in a common sheath of connective tissue" (Wilder).

The reversible diagram shown in Figure 123 shows quite clearly this correspondence of parts. In the annelid position we see the mouth at *m*, from which the œsophagus arises, passing through the nervous system and connecting with the long straight gut, *HH*, which terminates at the posterior end of the body at the anus, *a*. The nervous system consists of the large supraœsophageal ganglion or brain from which nerve connectives run, one on either side of the œsophagus, to the ventral nerve chain. The main blood-vessel lies dorsal to the gut and another lies beneath it. These are

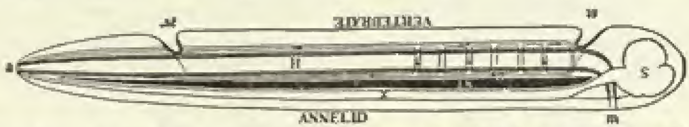

FIG. 123.—Reversible diagram illustrating the annelid theory of vertebrate origin. Reversible symbols, applying to both forms: *H*, alimentary canal; *S*, brain; *X*, nerve cord. Annelid symbols: *a*, anus; *m*, mouth. Vertebrate symbols: *NT*, notochord; *pr*, proctodæum (anus and rectum); *st*, stomodæum (mouth and pharynx). (After Wilder.)

connected in the anterior region by semi-circular pulsating vessels or "hearts" which cause the blood to flow forward in the dorsal vessel and aft in the ventral one. Reverse our diagram and the form becomes a vertebrate, the blood now flowing forward in the pulsating ventral aorta which serves as a heart, the ancient semi-circular "hearts" having relinquished their primal function for that of respiration, since the gill-slits arising between them make them the branchial vessels. As in the annelid, the mouth is again on the ventral side and this can only be brought about through the abandonment of the old and the formation of the new one by an inpushing of the body-wall at *st* until communication with the gut is effected. This stomodæum (Gr. στόμα, mouth, and δαίειν, to divide) is balanced at the hinder end of the trunk by the new hind gut, the proctodæum (Gr. πρωκτός, anus), *pr*, the ancient intestine in the tail region being aborted.

The brain and nerve cord are the homologues of the supraœsophageal ganglion and ventral nervous chain of the annelid. Indica-

tions of the ancient mouth are seen in several structures such as the neuropore in the embryo of *Amphioxus,* which forms in this place a direct communication between the cavity of the nerve cord (neurocœle) and the exterior and is otherwise unaccounted for. Other indications of the early mouth and its œsophagus are the fourth ventricle of the brain, a cavity which lies exactly in the place where in the diagram the annelid œsophagus pierces the nervous system, and also the hypophysis, a structure attached to

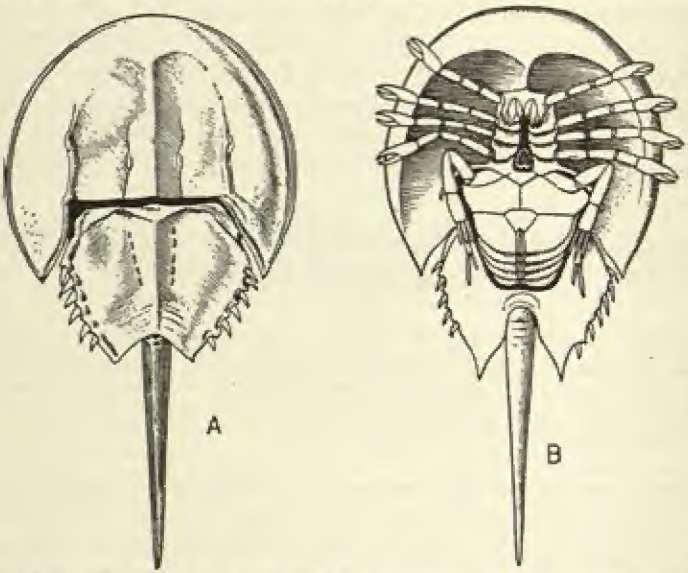

FIG. 124.—Horseshoe crab, *Limulus.* A, dorsal, and B, ventral aspect. (After Leuckart, from Parker and Haswell.)

the lower side of the mid-brain, part of which is pushed up from the alimentary canal, and for which there is as yet no satisfactory explanation.

Add to all this the remarkable correspondence of the kidney tubes or nephridia of the annelids and vertebrates, and the evidence is presented. Wilder says in summation: "Convincing as these comparisons seem when taken by themselves, the influence of later investigation has tended rather away from the annelid hypothesis, and at present, although there are many investigators who seek the ancestor of vertebrates in some worm-like form, there are few who wish to definitely assert that this ancestor was an annelid."

Arthropod Ancestry.—In addition to the annelid theory, some authorities have tried to prove vertebrate descent from Arthropoda, especially from the more primitive arachnoids such as are now represented by the scorpion and the horseshoe crab (*Limulus*, Fig. 124) and formerly by the extinct Merostomata (Fig. 125). By this hypothesis we must set aside as primitive such forms as *Amphioxus* and the cyclostomes and start with the highly specialized ostracoderms which lived in Ordovician and Devonian times and thus were contemporaneous with and in general appearance and probable habits quite similar to the Merostomata. The soft parts of the Merostomata are of course unknown, but it is reasonable to suppose that they were not unlike those of the related scorpion and *Limulus*, and, as Patten has shown, especially in the brain and cranial nerves of vertebrates and the fused cephalothoracic ganglionic mass found in such arachnoids, there are many points of resemblance. Then, too, the sense organs, especially the eyes, are more or less comparable, and there is in *Limulus* an internal skeletal piece known as the "endocranium" or sternum which serves to protect the central nerve complex, and which in general form and in its relation to other parts resembles the primordial vertebrate skull. Similarities also exist between the heart and arterial systems of each group, and the appendages may be compared. There are, again, the very arthropod-like jaws which Patten has demonstrated in the ostracoderm *Bothriolepis*, a type which, on the other hand, shows many vertebrate-like characteristics; and the general arrangement of the plates by which the cephalothorax is covered is also very similar in the ostraco-

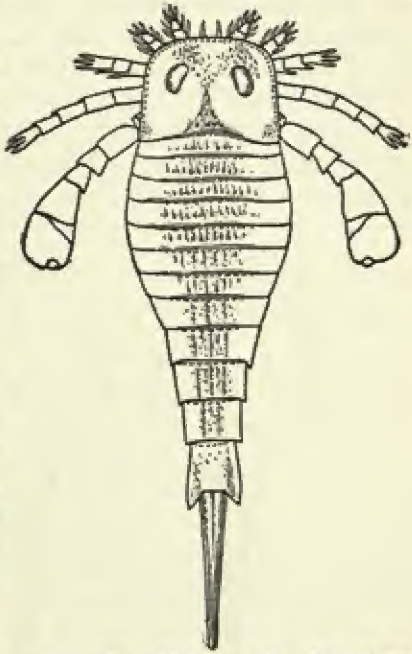

FIG. 125.—Merostome, *Eurypterus fischeri*, Silurian. (After Nicholson and Lydekker, from Parker and Haswell.)

derms and contemporary arachnoids, but unfortunately for the argument *Bothriolepis* is a highly specialized end-form from the Upper Devonian. Nevertheless, while the arachnoid theory has been set forth by Gaskell (*The Origin of Vertebrates*, 1908) and by Patten (*The Evolution of the Vertebrates and Their Kin*, 1912), the main thesis has received thus far but little recognition, although the evidence, especially in Professor Patten's book, is based upon an admirably executed piece of research.

Amphioxus Ancestry.—The theory of Amphioxus ancestry places especial emphasis upon the notochord, the gill-slits, and the dorsal position of the central nervous system, and by means of these has traced the line of vertebrate ancestry through a series of transitional forms, externally very unlike one another and each somewhat isolated in its systematic position (Wilder). Of these, *Am-*

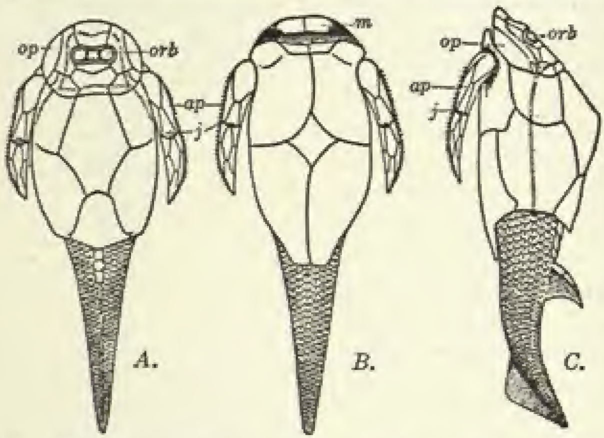

Fig. 126.—Ostracoderm, *Pterichthys milleri*, Lower Old Red Sandstone, Scotland. A, dorsal, B, ventral, and C, lateral aspects. *ap*, pair of lateral appendages; *j*, joint in appendage; *m*, supposed upper jaw, with notches for narial openings; *op*, operculum; *orb*, orbits. (Restoration by Traquair.)

phioxus, the lancelet, stands nearest the true vertebrates, in fact it is nearest the diagrammatic vertebrate of any living type, although, owing to certain specializations, it can hardly be considered a true stem-form. The lancelet was first described in 1778 as a shell-less snail or slug, and was named *Limax lanceolatus*. It is an inhabitant of the shallow sea (see page 55), being found off the coasts of all parts of the world. There are sixteen known species most of which are recorded from tropical and *sub-tropical* shores,

mainly between latitudes 40° N. and 40° S. In habits they are very sedentary, living for the most part partly buried in the sand or mud in a nearly erect posture, with the anterior end protruding. Aside from their primitive character, their world-wide distribution, coupled with sedentary habits, points to a very great antiquity. As fossils, however, they are thus far entirely unknown and probably always will be.

Description of Amphioxus (see Fig. 122).—The body is lanceolate, compressed, without a distinct head, but with an expansive hood-like structure surrounding the mouth, which is situated beneath the snout. There are no paired fins; but a pair of longitudinal folds, the metapleures, one on either side of the body along the ventral margin, suggest their possible origin. There is a slight median fin running along the back and supported by delicate skeletal elements membranous in character. Around the tail this fin expands into a caudal which extends forward on the ventral side beyond the anal opening, thus displacing the latter to the left of the median line.

A conspicuous feature is the regular segmentation of the muscular system, plainly visible through the transparent skin, the side muscles being divided into a large number (64±) of V-shaped myomeres (Gr. μῦς, muscle, and μέρος, part), each with the apex pointing forward. These do not precisely correspond on the two sides of the animal, and by their successive contraction and relaxation they produce the undulatory movement of the body by means of which locomotion is effected. The notochord has already been described and also the fact of its continuation to the extreme end of the snout, instead of ceasing beneath the midbrain as in all higher vertebrates (Craniata).

Lying along the dorsal side of this notochord and enclosed with it in a connective tissue sheath is the central nervous system, comparable to that of fishes except that it lacks an expanded brain other than a slight enlargement. The only definite sense organs are an olfactory pit on the left side and a single median pigment spot which serves for the perception of light transmitted through the transparent body.

The alimentary canal lies beneath the notochord, and consists of the mouth and a large pharynx that extends more than half the length of the body and is pierced by numerous gill-slits. The intestine runs directly backward, terminating in the laterally situated anus. There also arises from it ventrally a hollow outpushing known as the liver.

The circulatory system is comparable to that of other vertebrates but is much simpler, and the heart is represented by a pulsatory ventral aorta lying beneath the pharynx. The blood, however, is colorless.

It will thus be seen that *Amphioxus* is a very simple "vertebrate," specialized a little along certain lines, but with several structures of such fundamental importance that they must be

borne in mind in our search for yet more primitive forms. These structures are the notochord, the dorsally situated nerve cord, and the pharynx perforated by gill-slits and provided with an endostyle.

The only other living creatures (except *Balanoglossus*, see page 435) which possess these structures during any part of their career are the *tunicates*, some of which are planktonic, others meroplanktonic, in that while they have active larvæ they soon settle down and become wholly sedentary in their habits. These sedentary forms, curiously enough, have retained more of their primitive characters than those which are planktonic, as their larvæ are comparatively undifferentiated. The free-swimming forms, on the other hand, are often modified in a remarkable way and may have so complex a life-history that the old-time chordate characteristics have almost entirely disappeared, They always, however, possess the gill-slits except in certain locomotive individuals among the colonial types, which have lost all organs except those of propulsion, that is, the muscles, nerves, and sense organs. The name tunicate comes from the test or tunic which surrounds the entire animal and is comparable to the shell of a mollusc in that it is formed by the body-wall or mantle. This test is unique in being made up of a substance closely comparable to the cellulose of plants.

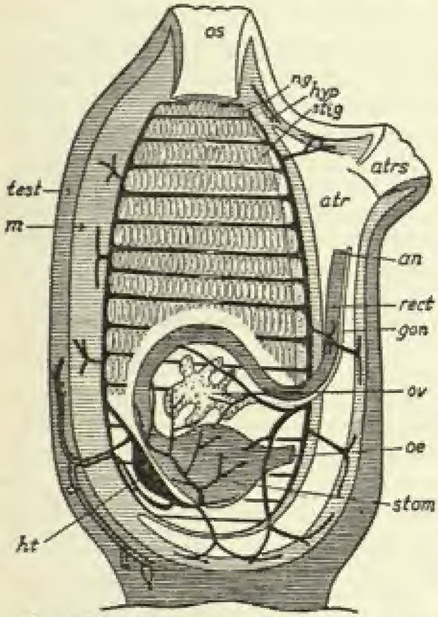

FIG. 127.—Tunicate, *Ascidia*. Diagram of longitudinal section from left side. Test and mantle removed. *an*, anus; *atr*, atrium; *atrs*, atrial (exhalent) siphon; *gon*, gonoduct; *ht*, heart; *hyp*, hypophysis; *m*, mantle; *ng*, nerve ganglion; *œ*, œsophagus; *os*, oral (inhalent) siphon; *ov*, ovary; *rect*, rectum; *stig*, stigmata (pharyngeal perforations); *stom*, stomach; *test*, test or tunic. (After Parker and Haswell.)

While the adult tunicate shows certain *Amphioxus*-like charac-

teristics, it is the larva in which these are particularly emphasized, for in this stage the creature, which is tadpole-like, possesses a well developed notochord, segmented muscles, and a prolonged nerve tube with a brain-like vesicle forward which contains a pigment spot and another organ, possibly for balancing. The gill-slits are much fewer in number than in the adult and the endostyle lies in its normal position. The heart also lies ventrally and just behind the œsophagus.

But this comparatively high organization is retained for a very brief time, a few hours only. Then the creature settles down on a pair of adhesive papillæ and undergoes a marked retrogressive metamorphosis (see Fig. 23) during which it loses tail, notochord, and segmental muscles; the nerve tube is reduced to a single ganglion, the sense organs disappear, the gill-slits increase in number, and the animal, after relinquishing practically all of the organs that serve to link it with the vertebrates, degenerates into what is virtually an invertebrate form. It is, however, evident that the tunicates represent a group more or less closely allied to *Amphioxus*, and hence to the other vertebrates, but that since the time of the common ancestor they have taken a divergent road, resulting in a type of degenerate adult whose real affinities are masked by its specializations. Thus, as Wilder says, "The ancestor that we here seek is better seen in the larva than in the adult, and we may believe that there once existed an adult animal with attributes like that of the tunicate larva of the present day, and that this animal was the direct ancestor of that group of which *Amphioxus* is now the only living representative."

Back of the tunicate ancestor there is but one known form which may or may not be near the main ancestral line. This creature is *Balanoglossus*, a marine worm that lives between high and low water marks in fragile tubes of cemented sand.

Balanoglossus is elongated without internal segmentation, but the body is divided into four regions (see Fig. 128), the burrowing proboscis, a collar with a free anterior edge, a flattened gill region, and a posterior trunk. The mouth is situated just beneath the edge of the collar on the ventral side and receives sand with its contained organic débris. There is a large pharynx communicating with the exterior by two lateral rows of gill-slits supported by a skeletal structure comparable to that seen in *Amphioxus*. Owing to the fact that nowhere except among the chordates do such structures occur, naturalists have sought in this animal for the other two chordate characteristics, the notochord and dorsal nervous system. The latter

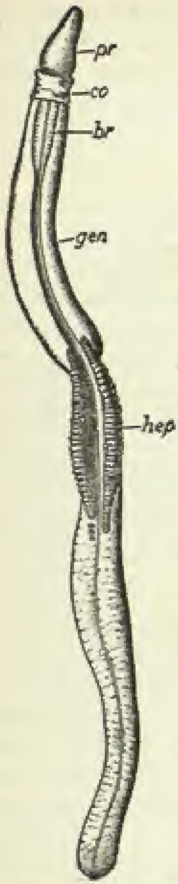

FIG. 128.—*Balanoglossus. br*, gill region; *co*, collar; *gen*, genital ridges; *hep*, prominences formed by hepatic (liver) cæca; *pr*, proboscis. (After Spengel, from Parker and Haswell.)

is apparently represented by a very generalized system of nerve fibers and cords somewhat emphasized on the dorsal side, but there is no evidence of the neurocœle. The notochord is supposed to be represented by a small outgrowth arising from the dorsal wall of the pharynx and extending forward into the proboscis. As Wilder says, this supposition has been greatly strengthened through the recent discovery of an allied form belonging to a new genus (*Harrimania*) in which the outgrowth is much larger, and, in its mode of origin, strikingly similar to the true vertebrate notochord, and thus without much doubt homologous with that organ. Wilder further says:

"From the testimony afforded by the structure of *Balanoglossus* and its allied genera (the group Enteropneusta) it may be quite confidently asserted that these forms lie nearly in the line of vertebrate descent, and represent an earlier stage than that of the tunicates. But here the chain seems to end, for *Balanoglossus* is itself unusually isolated and shows no close affinity to any other invertebrate types."

There is but a single rather slender clue to the ancestry of *Balanoglossus*, and that is again afforded by its embryology, for here there is a peculiar ciliated larva, the so-called *Tornaria*, which shows a very marked resemblance to the larvæ of the echinoderms (Fig. 129), and the universal occurrence of this larva within the latter group shows that, whereas they are all to-day, with rare exceptions, either sedentary or vagrant benthos, as their radial symmetry implies, they are descended from a pelagic bilaterally symmetrical ancestry. Thus, according to this belief we may "accept as a very ancient common ancestor of both echinoderms and vertebrates the form which all these larvæ may be said to copy; a form having the characteristics common to all, including bilaterality, minute size, transparency, locomotion by bands of cilia, and pelagic life. The lineal descendants of this hypothetical ancestor chose two paths, the one leading to the Echinodermata, the other to *Balanoglossus*, the Tunicata, *Amphioxus*, and eventually the Vertebrata" (Wilder).

While this theory is incomplete in many details, it has strength where the other hypotheses are weakest in that it is based not alone upon adult structure but upon ontogeny as well. The weakest link in the chain of evidence is that which binds *Balanoglossus* to the echinoderms—the *Tornaria* larva—because the adult structures

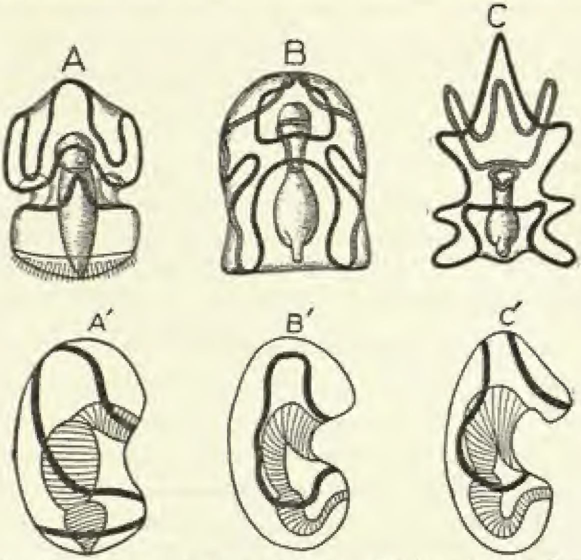

FIG. 129.—Comparison of *Tornaria* larva with larval echinoderms. Main ciliated bands in black, lesser systems cross-lined. Ventral aspect: A, *Tornaria;* B, *Auricularia* (sea-cucumber); C, *Bipinnaria* (star-fish). Lateral view: A′, *Tornaria;* B′, *Auricularia;* C′, *Bipinnaria.* (After Wilder.)

are so remote and the echinoderms give not the slightest clue in their bodily make-up to chordate affinities. As Matthew says: The origin of chordates "is still an unsolved problem. We cannot yet point to our ultimate ancestor in the Cambrian fauna. But whether known or unknown, and the latter is by far the more likely hypothesis, we can be pretty sure that we *had* an ancestor at that time, and that his evolutionary status was not above that of the trilobite, and may have been no better than a worm."

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CHAPTER XXIX

EMERGENCE OF TERRESTRIAL VERTEBRATES

Next to the origin of the vertebrates from their ancient ancestry, the greatest and most dramatic event in all their history is the emergence from the old limiting aquatic environment and the subsequent adaptation to land-dwelling life. The sea is so changeless and the range of its conditions so small that evolution within it is not stimulated as it is on land. Adaptive radiation of marine creatures can accomplish but little; we have seen, on the other hand, what it means on the part of air-breathing forms.

Place of Emergence

The three problems which come to mind are the place, the impelling cause, and the time of this important event, and of these the first has been established, for while certain creatures have forsaken the sea and, crossing the strand, become adapted to terrestrial life, such instances are rare and in no case do they embrace all of the members of a class or phylum, but isolated genera or even species only. Such, for example, are the land crabs, *Birgus latro*, etc., several species of which live in damp woods far from all water and, as they are found on islands which, like the Dry Tortugas, have no permanent terrestrial waters, must have had their initial air-breathing adaptation along the strand. The terrestrial vertebrates, however, apparently did not so emerge, but rather were descendants of inhabitants of land waters, for in such a habitat alone can we find a sufficiently great impelling cause for an event so far-reaching and radical in its ultimate results. Furthermore, the ancestral habitat could not have been within the limits of the tidal zone but was beyond the influence of the sea.

Impelling Cause

Enemies in the Water.—Barrell has discussed the probability of several possible causes which may have led to the emergence of the vertebrates. Of these, the first is enemies in the water, which he deems inoperative, for among land-going fishes of to-day those

few which crawl on land do not do so to excape their enemies. He also emphasizes the balance which always obtains between carnivorous and herbivorous creatures of a given habitat, and the fact that the amphibia go back to the waters to bring forth their young, and the youngest and therefore the most helpless stages are spent in the waters. Add to this the fact that the earliest amphibia which are known from their skeletons, and their ancestors, are, in many instances, powerful armed carnivores themselves, and their forsaking of the ancient habitat for personal safety seems hardly adequate.

Food on the Lands.—Food on the lands is also considered an inadequate cause. Here the argument lies in the rarity of the passage of crustaceans, gastropods, and vertebrates from a truly marine to a truly terrestrial mode of life through the ever present path of the tidal zone, which seems to prove that the unused though increasingly abundant food of the land realm cannot operate as a sufficient cause for this change, nor, so far as this factor is concerned, do the river faunas have an advantage over those of the tidal zone.

Lure of Atmospheric Oxygen.—That the lure of atmospheric oxygen is also inoperative is proved by the small direct use made of air for respiration by pelagic marine fishes even when they—the flying fishes, for instance—live an active life near the surface and in frequent contact with the air. It is principally in fresh-water fishes that accessory respiratory organs are employed and their use is in direct relation to the varying impurity of the waters in which they live. This varying impurity, which often means a reduction of respirable oxygen in the water, is literally impossible in the sea. Streams may locally contaminate the adjacent waters by their load of sediment or other impurities, but they cannot seriously lessen the degree of aëration. Then, too, marine fishes are never confined to such localities, but can migrate should conditions become unsuitable; while with fresh-water fishes this may not be true.

Recurrence of Unfavorable Environment.—The real cause, therefore, seems to be not the need of safety or food, nor the desire to breathe atmospheric oxygen, but rather an adaptation which has been forced repeatedly to a greater or less degree upon fishes by the recurrence of an unfavorable environment. Hence it appears as though the emergence were compelled by variations in the

environment as measured by the amount of dissolved oxygen in the land waters, and the question arises whether such variations occur and, if so, under what climatic conditions. The required climate does occur in various parts of the world, but is neither arid nor humid, but semi-arid—conditions which are found in the tropics especially, where, instead of the fourfold change of seasons whose determining factor is temperature, there are alternate seasons of drought and copious rain, occurring in definite cycles. In such a region during the rainy season the streams would be high and fully aërated, but when the rains ceased the waters would gradually slacken their current, until instead of a flowing river of pure water there would be a succession of stagnant water pools, in which the concentrated plant and animal life would die and by its decay charge the waters with impurities and exhaust their free oxygen. Thus we would get a great fluctuation of oxygen content and so a very variable environment in its ability to support water-breathing life.

Under such conditions, if life existed, a high premium would be placed upon powers of æstivation, or torpidity induced by summer heat and dryness, or of breathing the atmosphere, or both combined; and a rapid elimination of the unfit, that is, of such as did not possess even the rudiment of this power, would occur.

Air-breathing Fishes

There are among existing fishes a number possessing supplementary respiratory organs which may be one of two structures: either (1) spongy outgrowths of the gills which can retain moisture and, as long as it is retained, utilize the free oxygen of the air for the aëration of the blood; or (2) a modified swim-bladder which may have one of several functions but whose principal purpose is a hydrostatic one—to maintain the fish at a given level in the water.

Teleosts.—The first of these structures, that of the accessory organ connected with the gills, is found exclusively in teleostean fishes, a group in which the air-bladder never subserves a respiratory function. Several such teleosts exist, among them the climbing perch, *Anabas scandens* (Fig. 130), and the mud skippers, *Periophthalmus* and *Boleophthalmus*, but they are generally fishes which voluntarily leave the waters for migration or in pursuit of food, and rarely is their evolution the result of adaptation to the environmental conditions postulated above.

The swim-bladder, on the other hand, is entirely absent in the two groups known as cyclostomes and elasmobranchs and, as we have seen, is never of respiratory value in the teleosts, so that its function in this direction lies in the groups between, in other words,

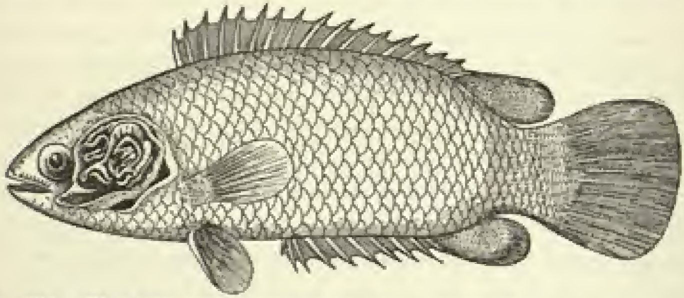

Fig. 130.—Climbing perch, *Anabas scandens*, with gill-cover (operculum) removed to show accessory respiratory organ. (After Jordan.)

among ganoids and dipnoans or true lung-fishes, and these fishes are to-day all denizens of semi-arid tropical climates, living under conditions of varied water aëration arising in the way we have described. These air-breathing fishes are of such importance to our argument, and are so few, and represent so ancient a group or groups that some account of the individual species is worthy of record. It should be borne in mind, however, that these are relic forms, representative of Devonian time when almost all fresh-water fishes belonged to one or the other of these two groups.

Ganoids.—The ganoids of especial note are specifically of the order Crossopterygii, or the lobe-finned ganoids, and include but

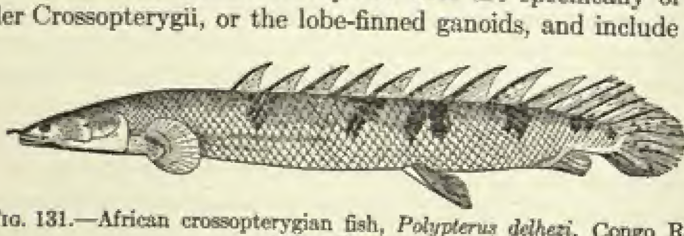

Fig. 131.—African crossopterygian fish, *Polypterus delhezi*, Congo River. (After Jordan.)

two related genera, *Polypterus* and *Calamoichthys*, both African in distribution. Of them the better known is *Polypterus* (Fig. 131), of which there are several species. *P. bichir* "haunts the deeper holes and depressions of the muddy bed of the Nile, although it is not essentially a bottom-liver or mud-fish. It is most active at

night when in search of food, and then it may readily be taken by trawl-lines. The lobate pectoral fins are used for progression, but their primary function is to act as balancers, and they exhibit the characteristic trembling movements so often seen in the balancing fins of teleosts. *Polypterus* does not readily live out of water, rarely longer than three to four hours, and then only when covered with damp grass or weeds. *P. bichir* is said to feed on small teleosts, which it swallows whole, and to these there may be added, in other species, batrachians and crustaceans. The observations of Budgett show that in captivity *Polypterus* often remains motionless for a long time at the bottom of the water, the anterior part of the body resting upon the tips of the pectoral fins. According to the same observer, the air-bladder is an accessory respiratory organ, supplementary to the gills, rather than a hydrostatic organ" (Bridge). This air-bladder is an out-pushing of the gut, and in the Crossopterygii arises from the ventral side of the gullet and is a paired structure exactly as in the amphibian lung. It is not, however, cellular and is thus a very inefficient respiratory organ.

In the genus *Calamoichthys* the body is elongate and eel-like in shape. The pelvic fins are entirely lacking but the pectorals and the series of dorsal finlets are comparable to those of *Polypterus* except that the latter are relatively fewer. *Calamoichthys* has a more restricted distribution than *Polypterus*, being confined to certain rivers in West Africa such as Old Calabar River and those of the delta of the Niger on the coast of Kamerun. It is a very agile fish, swimming like a snake and subsisting on insects and crustaceans. The name signifies palm-fish, from its frequenting the roots of the palm trees.

Neither *Polypterus* nor *Calamoichthys* is known fossil, but the group Crossopterygii to which they belong once included a large number of important fishes. Of these *Holoptychius* of the Devonian is interesting because of the intricate infolded structure of the teeth, which has a striking parallel in those of certain amphibia (labyrinthodonts). *Undina*, another form from the Upper Jurassic, exhibits a well developed air-bladder in the fossil specimen.

Dipnoans.—Of the dipnoans or true lung-fishes three genera only are extant but they never were as numerous as the Crossopterygii. The living forms are, first, the Australian genus *Ceratodus*, or, to be more accurate, *Neoceratodus forsteri* (Fig. 132), the barramunda, which is now confined to the Mary and Burnett rivers

in Queensland. This form "frequents the comparatively stagnant pools or water-holes which alternate with shallow runs and are usually full of water all the year round. In these pools, filled with a rich growth of aquatic vegetation, and often the favorite haunt of the platypus (*Ornithorhynchus*), the fish is fairly abundant. Inactive and sluggish in its habits, usually lying motionless on the bottom, the fish is easily captured by the natives with hand-nets or baited hooks. *Neoceratodus* lives on fresh-water crustaceans, worms, and molluscs, and to obtain them it crops the luxuriant vegetation of the water-holes much in the same way that a polychæt [worm] or a holothurian [sea-cucumber] swallows sand for the sake of the included nutrient particles. Apparently the air-bladder is a functional lung at all times, acting in conjunction with the gills. At irregular intervals the fish rises to the surface and protrudes its snout in order to empty its lung and take in fresh air.

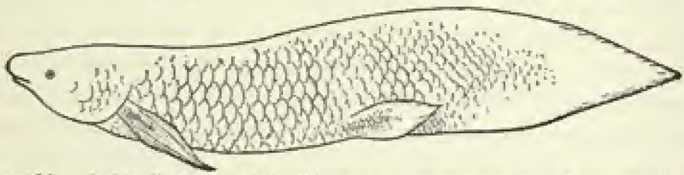

FIG. 132.—Australian lung-fish (dipnoan), barramunda, *Neoceratodus forsteri*. (After Dean.)

While doing so the animal makes a peculiar grunting noise, 'spouting,' as the local fishermen call it, which may be heard at night for some distance, and is probably caused by the forcible expulsion of air through the mouth. Useful as the lung is as a breathing organ under normal conditions, there can be little doubt that its value as such is much greater whenever gill-breathing becomes difficult or impossible. This seems to be the case during the hot season, when the water becomes foul from the presence of decomposing animal or vegetable matter. Semon records a striking instance of this in the case of a partially dried-up water-hole, in which the water had become so foul that it was full of dead fishes of various kinds. Fatal as these conditions were to ordinary fishes, *Neoceratodus* not only survived, but seemed to be quite healthy and fresh. Such observations are of exceptional interest. Not only do they afford a clue to the conditions of life which, in the course of time, probably led to lung-breathing in *Neoceratodus*, but they also suggest the possibility that a similar environment

has been conducive to the evolution of air-breathing vertebrates from gill-breathing and fish-like progenitors.

"In spite of its pulmonary respiration, *Neoceratodus* more closely resembles the typical fishes in its habits than any other Dipneusti. It lives all the year round in the water. There is no evidence that it ever becomes dried up in the mud, or passes into a summer sleep in a cocoon, and the well developed condition of its gills suggests that these organs play a more important rôle in breathing than in either *Protopterus* or *Lepidosiren*. The fish is not known to leave the water, and the paired fins, useful no doubt as paddles, are quite incapable of supporting the bulky body on terra firma. In fact, when *Neoceratodus* is taken out of its natural element it seems to be more helpless than most other fishes, and in spite of its capacity for lung-breathing, soon dies unless kept moist by artificial means" (Bridge). *Neoceratodus* grows to a length of five to six feet.

Ceratodus, a fossil ally, Mesozoic in age, was very widespread compared with the limited distribution of its living relative. Its very characteristic crushing teeth occur in the Trias of England, Germany, India, and South Africa, and also, more rarely, in the Upper Jurassic and Lower Cretaceous strata of England and in Colorado and Wyoming (Morrison formation). Its remains are often found associated with those of carnivorous dinosaurs, but the significance of this, if any, is not apparent.

Protopterus and *Lepidosiren*, which represent a separate family of lung-fishes, the Lepidosirenidæ, differ from *Neoceratodus* in that the air-bladder is a double organ, while in the latter it is single.

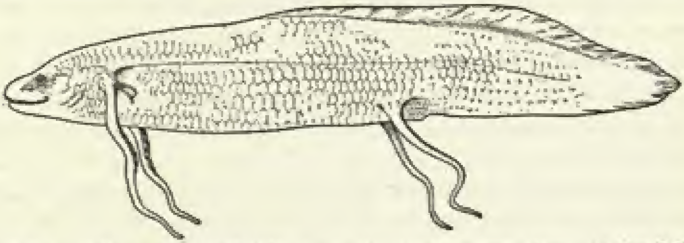

FIG. 133.—African lung-fish (dipnoan), *Protopterus annectans*. (After Miall, from Dean.)

Protopterus (Fig. 133) is the African lung-fish, and has a wide distribution ranging from the river Senegal and the White Nile on the north to the Congo basin, Lake Tanganyika, and the Zambesi on the south. The three known species live in marshes in the

vicinity of rivers. They are carnivorous, their food consisting mainly of frogs, worms, insects, and crustaceans, but when confined together they are very apt to display cannibalistic traits. The tail is the chief locomotor organ and they are remarkably agile and quick in their movements. The limbs are useless for swimming but are used for crawling over the bottom. Then they show a definite elbow- or knee-like flexure at about their mid-length. *Protopterus* ascends to the surface from time to time to breathe air into its lungs. In the dry season, however, it burrows into the mud to a depth of about 18 inches, where it forms a lining to the cavity in which it lies in the form of a capsule of hardened mucus secreted by skin glands. This capsule has an aperture the margins of which are pulled inward to form a short tube that is inserted between the fish's lips. The fish within the capsule is surrounded by a soft slimy mucus which keeps the skin moist, while respiration is effected by drawing the outer air through burrow and tube into the mouth and thence to the lungs. The lungs are, therefore, the sole means of respiration during the period of æstivation, while the body-fat and muscle-tissues of the fish, as in hibernating mammals, supply it with the necessary food. The dry season varies, but lasts in general from August to December, nearly half the year. When, with the advent of the rainy season, the marshes once more become flooded, the capsule is dissolved, *Protopterus* emerges from its burrow, and resuming its active life, very soon begins to provide for its coming young. The larvæ have much the appearance of a young salamander, with four pairs of external cutaneous gills and two pairs of simultaneously developed limbs. It also has chromatophores in the skin whereby its color may be changed. As in the salamander, the assumption of lung-breathing is marked by a reduction of the cutaneous gills, which takes place about seven weeks after the eggs are deposited. *Protopterus* attains a length of about six feet.

Lepidosiren, the mud-fish, with but a single existing species, is a South American form, occurring along the course of the main Amazon, entering some of its larger tributaries and also the Chaco Boreal to the west of the Upper Paraguay River. "The home of the *Lepidosiren* (or 'Lolach,' as the natives call the fish), of the Chaco country, is to be found in the wide-spreading marshes and swamps, which for a great part of the year are almost choked by a luxuriant growth of their own peculiar vegetation and covered by a

floating carpet of surface weeds, with here and there deeper and clearer water and slow-flowing streams. In the dry season the water gradually shrinks and the swamps eventually become dried up. Of sluggish habits, the fish wriggles slowly about at the bottom of the swamp like an eel, using its hind limbs in an irregular bipedal fashion as it wends its way through the dense network of subaqueous plants. *Lepidosiren* is not exclusively carnivorous. The large fresh-water snail *Ampullaria*, which lives in the swamps in enormous numbers, seems to be its favorite food; but masses of confervoid algæ are also eaten, and in its earlier stages it is probable that the fish is more herbivorous than carnivorous" (Bridge). *Lepidosiren* rises to the surface at intervals to breathe, the rate varying with the degree of impurity of the water. It feeds voraciously during the rainy season, storing up a supply of fat against the period of æstivation, which is passed in a deep tubular burrow, much as with *Protopterus*. The entrance to the burrow in this instance, however, is closed by a plug of clay perforated by several holes. On the coming of the waters the plug is pushed out and the fish escapes. Development is quite similar to that of *Protopterus* and in each case parallels the amphibia very closely. There are many other parallelisms of structure and habits between the two groups, so many in fact that, as Dean said, it is almost impossible to look upon them as of no greater significance than convergences.

Lepidosirenidæ are as yet unknown as fossils, but there is reason to believe that their evolution from the older Dipneusti has been in a manner retrogressive. *Dipterus*, the most ancient of lung-fishes, may be taken as a starting point and Dollo has selected a remarkable series of genera, *Scaumenacia*, *Phaneropleuron*, *Uronemus*, *Ceratodus* (*Neoceratodus*), *Protopterus*, and *Lepidosiren*, in which the evolutionary sequence agrees perfectly with their succession in time. Back of *Dipterus* lies an unknown ancestry, but one which probably falls within the group of crossopterygian ganoids of which *Polypterus* and *Calamoichthys* are the living representatives. The trend of evolution among the Dipneusti, if one may judge from *Lepidosiren*, is leading to an elongated eel-like type, which will be both limb- and scale-less, which may be indications of racial senescence. These two interesting groups of air-breathing fishes, the Crossopterygii and Dipneusti, are both on the eve of their racial passing. The lesson which they teach, however, is of great significance and brings us back once more to the theme

of our discussion—that of the most momentous emergence in prehistory; and our inquiry now leads us to a consideration of the probable time of emergence.

Time of Emergence

The evidence here is twofold: first, the fossil record, and second, the geologic evidence of climatic conditions such as we have assumed.

The fossil evidence, which will be reviewed in greater detail later, points to a time earlier than Upper Devonian, for it is upon sediment referable to that period that the earliest known footprint of a terrestrial vertebrate has been impressed. The time of emergence therefore cannot be later than the age of this footprint, and from the nature of things must somewhat antedate it, although how much we have no means of knowing, as it was a time of accelerated evolutionary change.

The climatic evidence points to the same result, for, as Barrell has shown by a careful study of the sediments and of other phenomena connected with the rocks of Devonian age, these were times of warmth and seasonal rainfall tending toward more marked semi-aridity of climate in the Upper Devonian. There is, moreover, a dominance of dipnoans and crossopterygians in the fish fauna. Of these fishes certain could and probably did adapt themselves after the manner of their living descendants to the increasingly long dry seasons, until the latter became so long that the period of activity was not sufficient for the creature's life needs. Then came the emergence, for instead of æstivation the animal must adopt some other mode of life which would prolong the time of its activity in spite of its climatic restrictions. Thus the more ambitious among the lung-breathers, not content with the limitations imposed upon their lives, emerged from the age-long aquatic home and ventured into the new and untried habitat. Many may have essayed the emergence, but it is probable that relentless nature, weeding out the less fit for so valorous an undertaking, destroyed all but a single sort, for there is no evidence that the ancestry of the amphibia is to be found in more than one evolutionary lineage.

Ancestry

In spite of the many similarities which exist between the Dipneusti and the amphibia, there are few authorities who hold to a

possible direct derivation of the one from the other, for very serious anatomical difficulties stand in the way, one of which is the very peculiar and specialized type of limb, the archipterygium, which this group of fishes possess, and out of which it is seemingly impossible to evolve the terrestrial hand or foot. The Crossopterygii, on the other hand, exhibit fewer of these obstacles; in fact, there are practically none which evolution cannot overcome. The general opinion, therefore, would derive the land-dwelling forms either from the Crossopterygii as such or possibly from some, as yet undiscovered, related group.

Changes upon Emergence

Partial Loss of Armor.—The essential changes undergone by the emerging form were, first, partial loss of armor, for while the earliest amphibians, the Stegocephalia (Gr. στέγειν, to cover, and κεφαλή, head) are armored, the armor is confined mainly to the head as the name signifies, to the breast girdle, and to oblique rows of small scales, chiefly on the under side of the trunk and tail. There is no evidence of their having possessed the heavy enameled scales of the ganoid ancestor.

Loss of Unpaired Fins.—The unpaired fins are of course strictly of aquatic use and their loss upon emergence is to be expected. They do, however, recur in forms which have returned to their ancestral habitat. Thus certain salamanders show a rather well developed caudal web of skin which in the male crested newt extends forward along the back, and many aquatic larvæ, those of frogs and toads, also have well developed unpaired fins. But these are new structures which have arisen in response to immediate need and bear no genetic relationship to the equivalent fins of fishes, the principal proof thereof lying in the fact that there is no trace in the amphibian of supporting fin-rays such as all fish fins show.

Development of Terrestrial Limb.—One of the most essential changes upon emergence was the modification of the paired fins of the fish ancestor to support the body on the mud, a function to which they were clearly inadapted in their original condition. The paired fins of the Dipneusti are, as we have seen, archipterygia, that is, having a long, jointed, bony axis, on one or both sides of which arose a series of parallel rays to support the fin membrane. Such a type of limb, while it may be used as a prop or for slow

crawling propulsion in a water-borne form, is in no known instance of suitable strength to support the entire weight of the animal when out of water, nor is it of sufficient surficial area to carry its owner over soft mud, for here a broad member is necessary. Then, too, the skeletal elements are such that one cannot see the slightest prophecy therein of the standard framework of the terrestrial foot.

With the crossopterygians, on the other hand, this is not true, for here the limb is different, having a broad basal lobe containing several bones and a fringe-like expansion so arranged that a much more adequate support is already present, even in the fish stage of evolution. It is particularly in the pectoral fin of the fish *Eusthenopteron* (Fig. 134), from the Devonian of Quebec, that the ter-

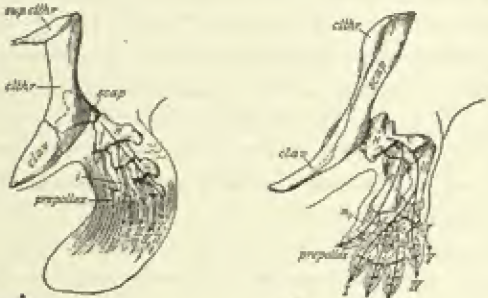

FIG. 134.—Left pectoral limb of A, *Eusthenopteron*, and B, *Eryops*. After W. K. Gregory. *H*, humerus; *R*, radius; *Scap*, scapula; *U*, ulna.

restrial limb is foreshadowed, the shoulder-bones corresponding bone for bone, the single proximal bone of the fin to the humerus, the next two to the radius and ulna, and the remainder, or some of them, to the bones of wrist, palm, and digits. Certain bones have naturally been lost and others added, and the entire fin-rayed portion of the limb abandoned with the relinquishment of the swimming function; but the whole metamorphosis requires no undue stretch of the imagination. The actual transitional limb is as yet unknown to us, but the most ancient footprint, *Thinopus* (Fig. 135), is apparently not that of a completely evolved foot and may thus throw light upon the process of evolution. This footprint, while giving no clue to the skeleton of the upper and lower arm and wrist, does give a very adequate idea of the digital structure, which is highly peculiar. There are but two completely

formed fingers, probably the first and second, the cleft between them extending deep into the sole of the foot. The phalangeal pads and a rounded, terminal, claw-like portion are already developed and there appears on the outer side of digit II the rudiment of a third, and below this on the outside of the foot the possible *Anlage* of digit IV.

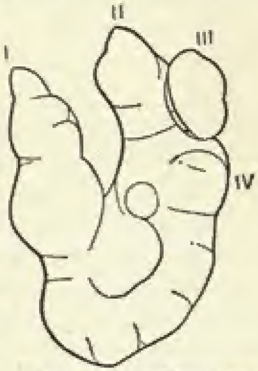

FIG. 135.—Earliest known fossil footprint, *Thinopus antiquus*, with two fully formed digits, I and II, a partially formed third, III, and a possible rudiment of a fourth, IV. Upper Devonian of Pennsylvania. One-half natural size. Original in Yale University Museum.

If this is a normal footprint, as we may suppose it to be, it seems to prove that the terrestrial foot, instead of being five-toed from the beginning—and that is certainly the standard undifferentiated type to-day—began as a two-toed organ on the outer side of which the remaining digits arose in orderly succession until the typical number was acquired and the member became standardized.

That this may have been the case is not alone evidenced by the unique footprint which we have discussed, but the arrangement of the nerves and muscles and the major and minor axes of the foot and limb are corroborative. The ontogeny of the salamander's foot as figured by Rabl (see Fig. 137) shows the same budding of the lateral digits as the *Thinopus* track implies. So that, without having seen the footprint, Professor Wilder as a result of his embryological studies postulated an ancestral foot strikingly like that of *Thinopus*.

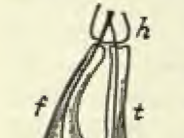

FIG. 136.—Foot of a reptile, *Ranodon sibericus*. *f*, fibula; *h*, femur; *t*, tibia; 1, 2, 3, 4, digits 1–4. (After Wiedersheim.)

Loss of Internal Gills.—The ancient fish gills, borne on the gill-arches, were also lost upon emergence, for in every instance where permanent gills are seen in living amphibia they are *external* dermal structures of later origin and not strictly homologous with the *internal* gills of the fishes. Some amphibian gills, it is true, *seem* to be internal, as they are occasionally covered by a fold of skin, the operculum, so that they thus come to lie in a gill chamber; but they develop

before the gill-clefts open, are restricted to the outer side of the branchial arches, and are always covered by ectoderm, all of which goes to prove them new organs which have assumed the old lost function of aquatic respiration.

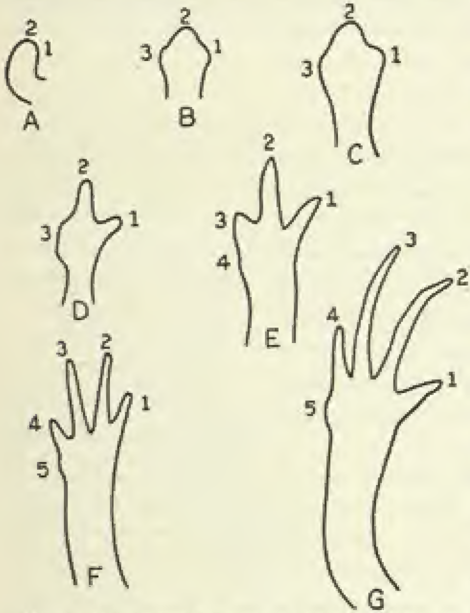

Fig. 137.—Development of the hind foot of a salamander, *Triton tæniatus*. (After Strasser, from Rabl.)

Fossil Record

Footprints.—The earliest record of a terrestrial vertebrate is the single footprint of *Thinopus antiquus* mentioned above. This is impressed upon a slab of sandstone and is from the uppermost Devonian (Chemung). It was found in 1896 by the late Professor Beecher of Yale and by him presented to the Museum where it is now treasured. These same beds contain ripple-marks and mud-cracks, and impressions of rain-drops and land plants also come from the same general horizon. A characteristic *marine* mollusc (*Nuculana*) is preserved on the under side of the footprint slab. The associated strata show dominant delta conditions on the outer margin of which the sea had contributed to the material, for in the wide oscillations of the strand-line characteristic of delta fronts, deposition under shore conditions and deposition under river conditions alternate (Barrell).

This Devonian is directly overlain by Lower Carboniferous (Mississippian) Coal Measures, represented in Nova Scotia and New Brunswick by the Horton series. These contain the remains of plants and crustaceans and the footprints of amphibians. No bones have been found in these beds, but the footprints indicate, at the beginning of the Carboniferous period and before the deposition of the Lower Carboniferous limestones, the presence of both

large and small species similar to those of the coal formation (Dawson). One interesting type, *Hylopus hardingi*, found in the Lower Carboniferous shales of Parrsboro, Nova Scotia, shows a stride five times the length of the foot and twice the width of the trackway, as though the creature which made it stood high on its legs like an ordinary mammal. This looks very much like a cursorial adaptation; if so, it is the earliest on record.

The next higher level to record the passing feet of these primal terrestrial forms is the Mauch Chunk series of Pennsylvania, assigned by geologists to the upper half of the Lower Carboniferous. Here has been recorded *Palæosauropus primævus*, a five-toed track of considerable size as these early forms run, and more careful search of these same beds at Pottsville has brought to light several other species, some very small and delicately impressed. Other tracks have come from Virginia and are referred to the same general age (Hinton formation).

An amazing series of footprints of Permian age representing a number of genera and species has recently come to light in the Grand Canyon, where they may be seen traveling up the strata until they disappear under the overhanging cliff. Some of these are preserved in the Yale Museum and some in the National Museum at Washington.

First Skeletal Remains.—The first amphibian bones were found in the Upper Devonian of Greenland and are comparable in age to that of the *Thinopus* footprint. Other skeletons come from the Edinburgh Coal Measures of Scotland which have been referred to the Lower Carboniferous. These are in no sense transitional forms, but are fully developed amphibians. Above the Lower Carboniferous Coal Measures we have red shales and sandstones in which bones are invariably rare and footprints abundant, and so it is with the Scottish record.

It was during Permian and Carboniferous times especially that the great deployment of amphibia occurred, and we have from various places, notably in Europe and in Nova Scotia and the United States, the remains of a varied assemblage of forms, some small, others huge, heavily armored types with complex vertebræ, still others with complexly infolded teeth; some with well developed crawling limbs, yet others limbless, elongate, indicating that already the condition which we have called racial old age, or senility, with its attendant degenerative specialization was upon

them. One and all were alike in this—they went, presumably, back to the waters to lay their eggs, and their young were therefore aquatic and breathed by means of gills (see Fig. 138). But there are among them many of which this cannot be proved and some may actually have been transitional, not between amphibians and fishes, but between amphibians and the succeeding class, the Reptilia. Certain of the forms, such as *Cacops* (Fig. 139), discovered in the Permian of Texas by Professor Williston, show such a combination of characters pertaining both to the amphibia and reptiles that, as the distinguished discoverer says, it may become necessary to revise our definition of the former group.

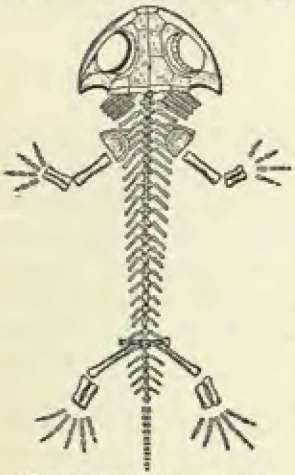

FIG. 138.—Stegocephalian, *Branchiosaurus amblystomus*, Permian, Germany. Restored larva, showing gill arches. (After Credner, from Eastman-Zittel.)

Summary.—"The nature of the geologic record of amphibians indicates that they evolved under climates marked by seasonal dryness, and inhabited river-plains far from the sea. The abruptness of appearance of well developed sustaining legs and feet points to an origin perhaps as far back as the Lower Devonian, but a rapid expansion and evolution in the Upper Devonian. They survived the change to more generally wet conditions in the Lower Mississippian, but showed more convincingly

FIG. 139.—Permian stegocephalian, *Cacops aspidephorus*, from Texas, allied to the primitive reptiles. (After Williston, from Schuchert's *Historical Geology*.)

their adaptation to semi-arid continental conditions through the footprint record they have left in the Mauch Chunk shales. The impressions of plants indicate that over the broad river-plains of eastern Pennsylvania there flourished each season an herbaceous

vegetation of acrogens following the withdrawal of the river floods, until the advancing seasonal dryness caused it to wither. No traces of an arboreal vegetation have been found, and this, taken in conjunction with other facts, suggests that in the dry season the streams completely vanished, or at least were reduced to rivulets and water-holes unable to afford sufficient underground water to support an arboreal vegetation on the banks" (Barrell).

Circumstances such as these were not conducive to piscine life, but were just the conditions under which amphibians would thrive. With further increase in aridity, however, such that no seasonal return of the waters occurred to make aquatic egg-laying possible, came the restriction of the amphibia and the evolution of reptiles.

Reptiles

Aside from certain anatomical characteristics, which we need not enumerate, two features stand out sharply in the reptiles in contrast to the amphibians. They are, first, the loss of gill-breathing forever, the reptiles and their descendants—the mammals and birds—depending solely upon their lungs for oxygen; and second, the development of certain embryonic envelopes known as the amnion and allantois. The true significance of both loss of gills and gain of allantois is the same—air-breathing young.

Embryonic Membranes.—The reptilian egg is a complex structure consisting not only of the male and female germ-plasm but of a considerable amount of nutritive yolk, sufficient to carry the creature well along toward perfection of body and obviating the necessity of a larval stage and a metamorphosis such as so many amphibians possess. This complex egg is surrounded by a protective envelope, the shell, and is invariably laid on land, if laid at all. It is because of this last feature that the amnion and allantois have arisen (Fig. 140). The amnion is a two-layered membrane growing out of the ventral wall of the embryo and entirely enveloping it. Between the layers is the amniotic fluid which not only guards the creature against mechanical jars but also serves to resist sudden changes of temperature which might be fatal to the growing young. In other words, the amnion is protective in its function. The allantois, on the other hand, is respiratory. It too is a double-layered or sac-like membrane arising in much the same way, an outgrowth in fact of the urinary bladder of the amphibian. It is abundantly supplied with blood-vessels directly continuous with

those of the embryo. The allantois lies, in its full development, immediately beneath the porous shell, through which oxygen can enter and, passing by osmosis through the allantoic membrane, oxygenate the included blood. Carbonic acid gas is given off at the same time. The blood stream now carries the oxygen to the embryo and brings out more waste and the process is continued. Thus it will be seen that the allantois has a function comparable to a lung and not to a gill, and it is to be doubted whether any reptilian egg could be placed in the water without drowning the embryo within. At all events, no reptile, bird, or mammal egg, each of which possesses an allantois, is ever laid in the water, but always on land, or else provision is made for its retention within the maternal body as in certain snakes, the ichthyosaurs, and all mammals above the Monotremata.

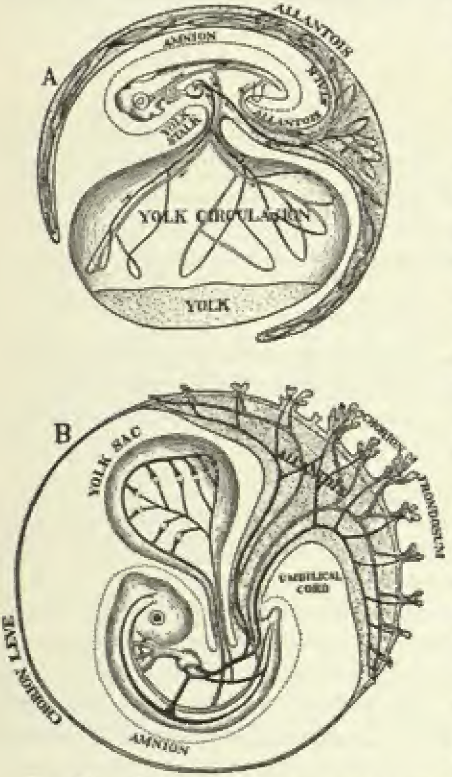

FIG. 140.—Vertebrate embryos with their membranes. A, reptile or bird; B, placental mammal. In A the yolk-sac is functional and the allantois respiratory; in B the yolk-sac is functionless and the allantois becomes the nutritive placenta and umbilical cord. (After Wilder.)

From this it will be seen that reptiles may survive under conditions of aridity—many are true desert forms—where amphibia might perhaps live as adults but could not pass on their life to future generations. It is logical, therefore, to believe that whereas semi-aridity with seasonally recurring rains impelled amphibian evolution, true aridity with undependable rains or none at all, making amphibian economy impossible, stimulated the evolution of the reptiles.

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CHAPTER XXX

RISE OF REPTILES AND DOMINANCE OF DINOSAURS

Origin of Reptiles

The origin of reptiles from their ancient stegocephalian lineage took place in all probability in Carboniferous time, and before the close of the Permian many of the principal lines of evolution had become established. The evidence for this belief is partly direct, through the Permian paleontological record, and partly indirect, based upon the appearance in the Trias of groups which must have had a long antecedent evolution.

The Permian strata record the actual presence of no fewer than seven out of the fifteen orders of reptiles which formerly existed, and while most of them are primitive forms as one would be led to expect, one group, the Mesosauria, represented by *Mesosaurus* (Fig. 141) from Brazil and South Africa, is noteworthy in being the first instance of the many which occur of the return of reptiles to the aquatic habitat. Yet more remarkable is the order Pelycosauria, particularly the so-called fin-back reptiles, among which certain genera have developed riotous growth, especially in the spinous processes of the vertebræ, some of which are extraordinarily long while others have lateral processes developed on the spines like the yardarms of a square-rigged ship (*Edaphosaurus*, Fig. 142). These fin-backed forms can be viewed in but one light—they are racially senile, and their utter absence from overlying strata points to their speedy extinction.

In addition to the seven recorded orders there is reason to believe, on the grounds mentioned above, that at least six, possibly seven, others had Permian representatives. These are the Chelonia or turtles, the Sauropterygia or plesiosaurs, the Ichthyosauria or fish lizards, the Squamata (lizards only), the Rhynchocephalia or beaked reptiles, the Thecodontia or crocodile-like, and possibly the dinosaurs. Among these several are aquatically inclined, others terrestrial. The former have been discussed in part in the chapter on aquatic adaptation (Chapter XX), the latter, especially the

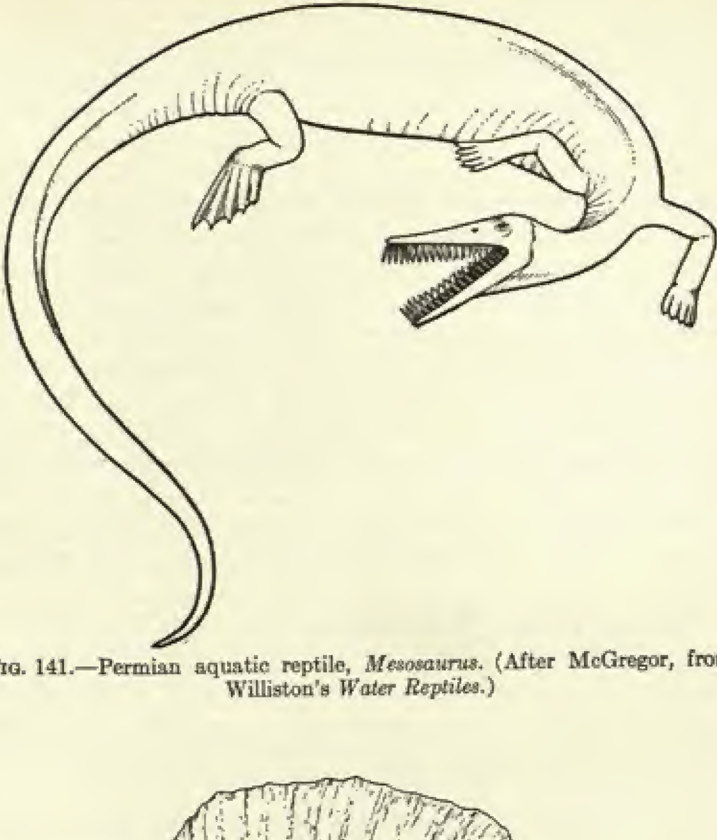

FIG. 141.—Permian aquatic reptile, *Mesosaurus*. (After McGregor, from Williston's *Water Reptiles*.)

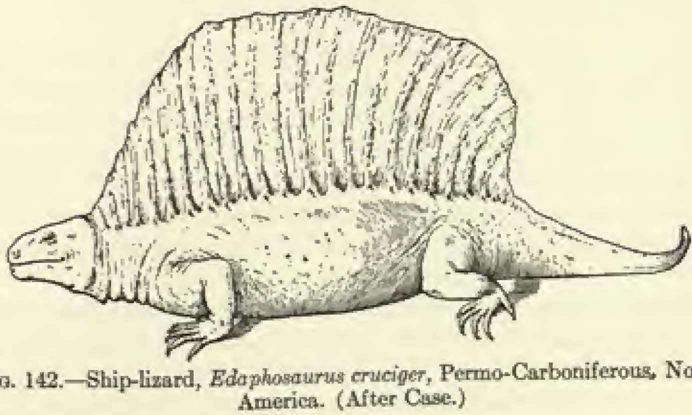

FIG. 142.—Ship-lizard, *Edaphosaurus cruciger*, Permo-Carboniferous, North America. (After Case.)

dinosaurs, will constitute the main theme of the present chapter and the next.

Adaptive Radiation of Reptiles

The Mesozoic era has been called the Age of Reptiles, for while higher forms, the birds and mammals, make their appearance during its course, arising in all probability when the era was yet young, they never seriously dispute with the reptilian horde their right to a place in the sun, in fact to all places wherein an animal could live. Thus the law of adaptive radiation, which originally was applied to the mammals, is equally applicable to these cold-blooded forms, for climatic zones were non-existent or but slightly differentiated and hence did not limit their poleward distribution as they do now, and, as a consequence, of the various habitats which the wide world displays, each had its admirably adapted reptilian denizens just as the world was later filled with mammalian hosts.

Central Form.—The central form was doubtless a short-legged, crawling cotylosaur, such as *Limnoscelis* (Fig. 143), a slow moving,

FIG. 143.—Restoration of the Permian reptile, *Limnoscelis paludis*, from New Mexico. (After a model by Lull.)

primitive, probably swamp-dwelling type but potent in evolutionary possibilities. From the cotylosaurs there arose in the course of time other more strictly terrestrial creatures such as the lizards, many of which have attained high adaptation to speed requirements. Yet another ancient reptile, *Kadaliosaurus*, from the Lower Permian of Germany, was a long-limbed, doubtless cursorial form. The cursorial adaptation *par excellence*, however, lay with the dinosaurs, as their bones and footprints show.

Arboreal Habitat.—Arboreal habitat is difficult to prove on the part of any Mesozoic or older reptiles, for if any arboreal forms existed, their remains, in common with those of other forest-dwelling types, would have had little chance of natural entombment and subsequent preservation. But to-day the arboreal reptiles are numerous and varied; to realize this, one has but to recall the

geckoes with their adhesive padded feet, or the chameleons with syndactyl grasping hands and feet and prehensile tail described in Chapter XXI. There are authorities, moreover, whose belief in an arboreal ancestry for the birds is so firmly established that the presence of climbing reptiles even in the Triassic or earlier, while having no documentary evidence to its support, nevertheless is by them assumed *a priori*.

Aërial Adaptation.—Aërial or volant reptiles such as the pterodactyls were finely adapted to their habitat, ranging as they did from the size of a sparrow to the largest of nature's flying mechanisms, with ample powers both of varied and sustained flight, but their origin is lost through the imperfection of the record of Triassic life (see Figs. 78 and 79, Chapter XXII).

Amphibious Forms.—Of the amphibious forms there were many, for increasing humidity—and we have ample evidence of the waxing and waning of moisture—brought with it extensive areas the peopling of which awakened the water-dwelling instinct that had long been dormant in the reptilian blood. Thus we have as partially aquatic forms the turtles, ancestral plesiosaurs (Nothosauria), Parasuchia, Crocodilia, and many dinosaurs, such as the Sauropoda and Hadrosauria, or duck-bills.

Aquatic Adaptation.—Truly aquatic life claimed in the course of time certain turtles, the great marine ones of to-day and still greater ones (*Archelon*) of the Cretaceous, the plesiosaurs, mesosaurs, ichthyosaurs, sea-lizards (mosasaurs), the thalattosaurs, and sea-crocodiles or thalattosuchians (Fig. 60); in all, eight orders, either in their entirety or in large proportion.

Fossorial Adaptation.—Fossorial animals are rare as fossils, for while burial is a prime requisite to fossilization, self-burial rarely carries with it the necessary imperviousness to air to insure preservation. Hence we cannot point to a single ancient reptilian group as of extensive fossorial habits, although in the cotylosaurs and pelycosaurs there are certain forms whose powerful implied musculature of arm and leg points to digging powers of no mean degree. That any were wholly fossorial like certain living snakes (*Typhlops*) and limbless lizards (*Amphisbæna*) we have no proof.

Adaptive Radiation of Squamata.—Thus it will be seen that during pre-Tertiary times the reptilian adaptations were ample and varied; with the dawn of the Tertiary, however, came the final extinction of all but four reptilian orders, one of which is repre-

sented by but a single relic form (*Sphenodon*) found to-day only in remote New Zealand. This widespread extinction necessarily restricted the range of adaptation, though within the group Squamata, which embraces the lizards and snakes, we have a latter-day radiation comparable in a very modest way to the great reptilian radiation of the Mesozoic. For example, we may enumerate:

Ambulatory terrestrial: many lizards, horned toad.
Cursorial: *Chlamydosaurus*, the Australian frilled lizard.
Arboreal: chameleon (see Fig. 67), geckoes.
Aërial: *Draco*, the flying dragon (see Fig. 69).
Fossorial: *Typhlops*, *Uromastix*, amphisbænians (legless).
Amphibious: many serpents, some of the monitors, *Varanus* which is a living relative of the ancient mosasaurs, the Galapagos sea-iguana *Amblyrhynchus* (see Fig. 53), and others.
Aquatic: the sea-snakes or Hydrophinæ, all of which except one land-locked form in Lake Taal at Luzon, Philippine Islands, are marine and may be found many miles from land.

To-day the lizards are kept in their place largely by the mammals. Were the mammals, including man, entirely blotted out so that this control would be removed, it is conceivable that out of the lizard-stock creatures would arise as diverse in habits, size, and prowess as were the reptiles of the Mesozoic, and that another Age of Reptiles would be ushered in.

Dinosaurs

The Age of Reptiles may well be called the Age of Dinosaurs, for so far as terrestrial creatures go they were all-important, the other reptiles individually and collectively forming but the supporting cast to these stars in the great drama of medieval life.

Place in Nature.—That the dinosaurs were reptiles goes without saying, although their appearance, at any rate in the eyes of those who would restore them in the flesh, was sometimes so very similar to that of certain great mammals of to-day that the uninitiated often confuse relationships and think of *Triceratops* (Fig. 160), for instance, as merely a very huge and somewhat better armed sort of rhinoceros. As reptiles they were exclusively lung-breathing and had a large egg which they may or may not have laid before hatching. This is often merely a matter of family convenience as among certain snakes and we know that certain of the dinosaurs

were egg-laying. They were scaly or armored, this we know; whether they were cold-blooded or not is a debated question. Such activity as they must have shown seems to hint at a possibility of warm blood, and such a belief has met with some support, but in the tropical climate which their known habitat implies there was little more need of a heat-maintaining mechanism than there is in modern cursorial lizards, the Australian frilled lizard *Chlamydosaurus*, for instance. There is no evidence on the part of dinosaurs of a heat-retaining "clothing" such as the birds and mammals possess.

Living Relatives.—Of the forms now living, the crocodiles on the one hand and the birds on the other stand nearest the dinosaurs. When one comes to work out a concise technical description of a crocodile and place it beside that of a dinosaur, he will at once see the similarity of the two groups, for the only characters which are *not* common to both orders are the presence in the crocodiles of a false palate, merely a device for eating under water, found in other animals as well and the exclusion of the pubic element of the pelvis from their hip socket.

Ancestral Stock.—Dinosaurs, as befits their high estate, were of ancient lineage. One of our best authorities on dinosaurian phylogeny, Doctor Friedrich von Huene, derives them from the primitive cotylosaurian stock which arose in Carboniferous time and continued until the Trias. During Permian time there arose from the cotylosaurs the group Protorosauria, of which *Protorosaurus* is the type, and out of these in turn the Triassic Parasuchia. While all dinosaurs were derived from the same stock, they are considered diphyletic from their origin; that is, the Ornithischia and Saurischia (see page 467) are unrelated except through a common ancestry.

Duration.—The known record of dinosaurs extends from the Middle Triassic (Muschelkalk) to the very close of Cretaceous time. This is particularly true of the saurischian dinosaurs; the plant-feeding Ornithischia, on the other hand, do not appear in the fossil record until late Triassic (Rhætic) but are doubtless older, their subsequent duration being coextensive with that of the others.

Distribution.—Dinosaurs are first found in Germany, at Gogolin, Upper Silesia, but this does not necessarily imply that that was their original radiation center. On the contrary the belief has been expressed that one must go farther west, where a great continent is thought by some paleontologists to have extended across what

is now the North Atlantic basin, thus connecting Europe and North America, and that somewhere within the confines of this continent the dinosaurs arose and began their world-wide march of conquest. For they extend the world over, across the United States and into Canada; in Brazil, in Patagonia; from England, Belgium, France, and Portugal, to Germany and Austria; in far away India, even to Australia; in Africa in its central, eastern, and extreme southern part; and are now recorded in abundance and variety from Central Mongolia. Thus they were actually world-wide, except for New Zealand.

Habitat.—Their habitat was varied, but in all probability their initial evolution, that for speed, took place under stress of semi-aridity of climate, and their main lines were eminently terrestrial forms. With the changing climatic cycles, which came with the passage of time, came dinosaurian adaptation to humid conditions, at least on the part of those we know, so that at least two groups, Sauropoda and Hadrosauridæ, give evidence of an amphibious habitat. (See p. 465.)

Habits.—In habits the dinosaurs were nearly as varied as the mammals are to-day—carnivorous, some small, preying upon such feeble folk as they might overcome, others gigantic, the most terrible terrestrial devourers of flesh the world has ever seen. Again, others were herbivorous—some with feeble dentition, the food being drawn unmasticated down a most capacious throat, others with a dental apparatus for the reduction of the most resistant herbage such as would offer little promise of satisfaction to the living herbivores. In certain instances the teeth are greatly reduced, as in *Diplodocus* (Fig. 150) and *Stegosaurus* (Fig. 157), the reduction accompanying other signs of specialization. Yet others like *Struthiomimus* of the North American Cretaceous were utterly bereft of teeth. The dietary of such forms it is difficult to conjecture with any degree of certainty.

Size.—The minimum recorded size, that of *Compsognathus*, was about two and one-half feet, with the bulk of a domestic cat. The footprints of the Connecticut valley, however, record the existence of feet half as long as those of *Compsognathus*, hardly "terrible lizards" as the term dinosaur implies. The other extreme was reached by *Gigantosaurus* (Fig. 151) of East Africa, whose over-all length has been variously estimated by its Teutonic discoverers to be upward of 120 feet, but by Matthew not to exceed 80 feet.

SCHEME OF DINOSAURIAN RELATIONSHIPS

Nevertheless it was an animal of such robust proportions that its weight must have been about 40 tons—greater than that of any living animal except the larger of the modern whales.

Classification

The classification of the dinosaurs is still in a somewhat uncertain state, owing largely to the fragmentary condition of much of the material, especially that from abroad. A somewhat conservative grouping, listing the better known genera, follows:

Order SAURISCHIA (Carnivorous Theropoda and Amphibious Sauropoda)

Suborder CŒLUROSAURIA (Carnivorous Dinosaurs)

Podokesaurus—Triassic; Massachusetts.
Hallopus—Triassic; Colorado.
Cœlurus—Jurassic; United States.
Compsognathus—Jurassic; Bavaria.
Ornitholestes—Jurassic; Wyoming.
Ornithomimus—Cretaceous; Wyoming and Alberta.

Deinodonts—Giant Carnivores from Cœlurosaurian Stock:

Gorgosaurus—Cretaceous; Alberta and (?) Wyoming.
Tyrannosaurus—Cretaceous; Wyoming.

Suborder CARNOSAURIA (Megalosaurs, Carnivorous)

Anchisaurus—Triassic; Connecticut valley.
Zanclodon—Triassic; Europe.
Plateosaurus—Triassic; Europe.
Megalosaurus—Jurassic to Cretaceous; Europe.
Allosaurus—Jurassic; North America.
Ceratosaurus—Jurassic; Wyoming.
Dryptosaurus—Cretaceous; Wyoming and Alberta.

Suborder SAUROPODA (Amphibious Dinosaurs)

Cetiosaurus—Jurassic; Europe.
Brontosaurus—Jurassic; Western United States.
Diplodocus—Jurassic; Western United States.
Brachiosaurus—Jurassic; Wyoming.
Pleurocœlus—Jurassic; United States and Europe.
Titanosaurus—Cretaceous; Europe, Africa, and South America.
Gigantosaurus, Cretaceous; Africa.

Order ORNITHISCHIA (Predentata, Beaked Dinosaurs)

Suborder ORNITHOPODA (Unarmored Herbivorous Dinosaurs)

Nanosaurus—Triassic; Colorado.
Anomœpus (footprints)—Triassic; Eastern United States.

Camptosaurus—Jurassic; Western United States and ? Europe.
Iguanodon—Lower Cretaceous; Europe.
Hypsilophodon—Lower Cretaceous; Europe.
Corythosaurus—Cretaceous; North America.
Anatosaurus—Cretaceous; North America.

Suborder STEGOSAURIA (Armored Herbivorous Dinosaurs)

Scelidosaurus—Jurassic; Europe.
Polacanthus—Lower Cretaceous; Europe.
Stegosaurus—Jurassic; Western United States and Europe.
Palæoscincus—Cretaceous; Western North America.
Ankylosaurus—Cretaceous; Western North America.

Suborder CERATOPSIA (Horned Herbivorous Dinosaurs)

Protoceratops—Cretaceous; Mongolia.
Monoclonius and *Ceratops*—Cretaceous; Western North America.
Triceratops—Cretaceous; Western United States.
Torosaurus—Cretaceous; Western United States.

Contrast of Phyla.—The two main phyla of dinosaurs to which the rather unwieldy names of Saurischia (Gr. σαῦρος, lizard, and ἰσχίον, hip-joint) and Ornithischia (Gr. ὄρνις, bird) have been given, while undergoing in many ways a remarkable parallelism of evolutionary change, show notwithstanding some very constant contrasting features. These two orders may be thus briefly defined:

Saurischia: Generally carnivorous, except the Sauropoda, with teeth in the anterior portion of the mouth; compressed, slightly curved crowns with serrated margins, or spoon- or pencil-shaped teeth. Without predentary bone connecting the two halves of the lower jaw; with powerful, sharp-pointed, curved claws, and dense, hollow bones with well finished articulations except in the Sauropoda. Pelvis triradiate (see Fig. 144,B), with a hip-bone or ilium elongated fore and aft, a simple pubis directed downward and forward, and an ischium directed downward and backward. Includes the bipedal carnivores and the quadrupedal, amphibious, herbivorous sauropods.

Ornithischia (Predentata): Teeth in rear of jaws only, sometimes forming a wonderful magazine of successional teeth, and a toothless predentary bone in front which, with rare exceptions, opposed the equally toothless premaxillary bones above; premaxillary and predentary sheathed with horny skin or a turtle-like beak for the prehension of food. Limb-bones less compact and less well finished at their extremities than in the carnivores; claws depressed, some-

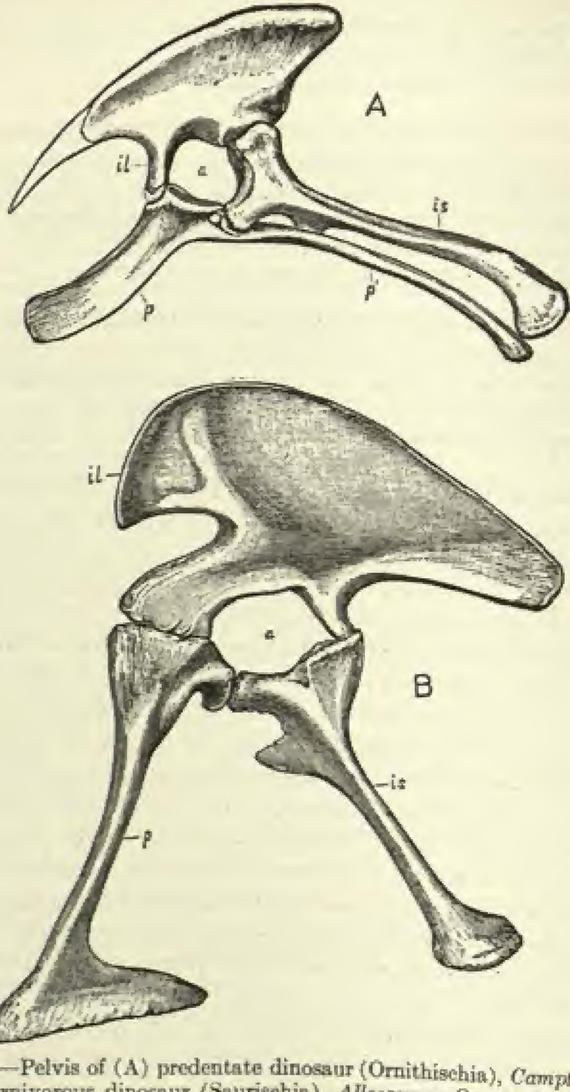

FIG. 144.—Pelvis of (A) predentate dinosaur (Ornithischia), *Camptosaurus;* and (B) carnivorous dinosaur (Saurischia), *Allosaurus.* One-twelfth natural size. *a*, acetabulum or hip socket; *il*, ilium; *is*, ischium; *p*, pubis; *p'*, post-pubis. (After Marsh.)

times hoof-like. Pelvis tetraradiate (see Fig. 144,A) in that the pubis normally consists of two branches, one of which, the prepubis, extends downward and forward, while the post-pubis lies parallel with the ischium. The ornithischian pelvis and the ossified tendons are quite suggestive of those of a bird; the saurischian, on the other hand, is more crocodilian.

Saurischia. Theropoda

The earliest known dinosaurs belong to the Saurischia, and they exist with conservative changes to the close of the Mesozoic. The principal evolutionary changes which they show are a gradual increase in size of body and a proportionate decrease in that of the fore limbs, the function of which in bipedal Theropoda is not locomotion, but prehension. These creatures therefore walked or ran entirely on the hind legs, the anterior part of the body being balanced by the weight of the long, slender tail. When they ran the limbs were well under the body and the stride was alternate like that of an ostrich or bipedal lizard, as their numerous bird-like footprints impressed upon the sands of the Connecticut valley imply. Some of the better known carnivorous dinosaurs are:

Cœlurosauria.—These are in general the smaller and more agile of the carnivorous dinosaurs which, Matthew thinks, were largely upland dwellers. As a rule their bones were hollow and the entire skeleton light and bird-like. Their range is from the Triassic to the close of the Cretaceous, and they are widespread, being found in Mongolia, as well as in North America. During the Cretaceous they diverge into two races, the ornithomimes or bird mimics, represented by *Struthiomimus* and *Ornithomimus*, some of which at any rate were toothless and doubtless of omnivorous habits; and a group of huge Carnivora, the deinodonts, which converged toward the megalosaurs and include among their number some of the most terrible devourers of flesh the world has ever seen. The culminating member of this subrace is *Tyrannosaurus*, described below.

Representatives of this group are: *Podokesaurus* (Fig. 145), an extremely slender, agile, carnivorous dinosaur from the Triassic sandstones of the Connecticut valley (South Hadley, Massachusetts). The body, tail, and limbs were preserved in the one specimen known, unfortunately destroyed by fire, and indicate an animal about four feet in length of which the tail includes more

than half. Many footprints described under the name of *Grallator* (he who walks on stilts) were undoubtedly made by creatures similar to this.

Cœlurus, with bones so delicate that the walls of the vertebræ, for instance, are of paper-like thinness. It was a small form from

FIG. 145.—Restoration of *Podokesaurus holyokensis*, Upper Trias, Connecticut Valley. Length, nearly four feet. (After a model by Lull.)

the Morrison formation of Wyoming and the Potomac formation of Maryland, and is incompletely known.

Compsognathus, known from a very perfect skeleton from the Jurassic of Eichstädt, Bavaria, and coming from the famous Solenhofen quarry which also produced *Archæopteryx*, the earliest known bird. *Compsognathus*, as has already been stated, is the smallest recorded dinosaur.

Out of the famous Bone Cabin quarry in eastern Wyoming, where the author was initiated into the mysteries of bone-digging, and which has produced *Allosaurus* (described below), comes *Ornitholestes* (Fig. 146), an extremely slender form whose total length was not more than 7 feet and whose bulk could not have exceeded that of a setter dog. This form had long, slender fingers none of which was armed with the cruel curved claws of the megalosaurs. This suggested the idea that perhaps it may have preyed upon

FIG. 146.—Restoration of the small carnivorous dinosaur, *Ornitholestes*, based upon a specimen in the American Museum of Natural History. Length seven feet. Jurassic, Wyoming. (After Lull, from Schuchert's *Historical Geology*.)

contemporary birds, so the name *Ornitholestes*, the "bird robber," was given to it. Another suggestion was that it may have preyed upon fish, and its association with amphibious dinosaurs lends color to the proposition. Be that as it may, the contrast between the marked agility of *Ornitholestes* and the more ponderous character of *Allosaurus* must have been reflected in the prey. A successor to the Jurassic *Ornitholestes* was *Ornithomimus* of late Cretaceous time, a form long known from its slender, very bird-like feet and a few other elements of its frame. The entire skeleton of an intermediate form, *Struthiomimus*, was discovered in Alberta in 1914. In its general proportions it is what one would

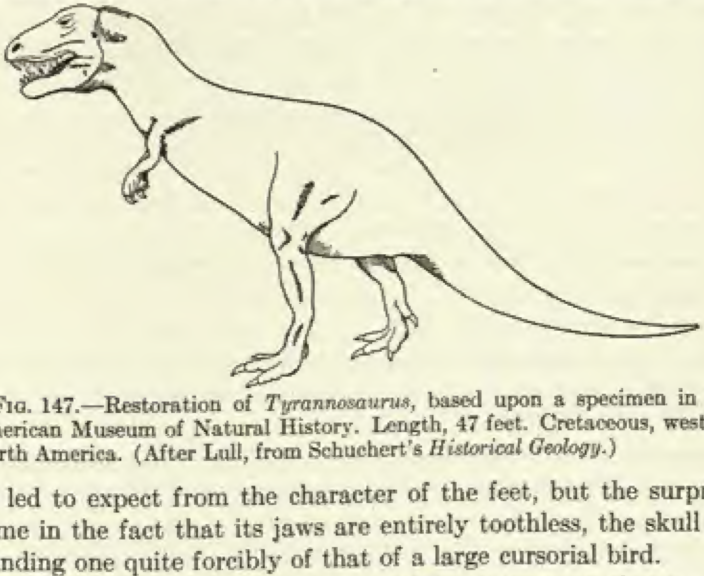

FIG. 147.—Restoration of *Tyrannosaurus*, based upon a specimen in the American Museum of Natural History. Length, 47 feet. Cretaceous, western North America. (After Lull, from Schuchert's *Historical Geology*.)

be led to expect from the character of the feet, but the surprise came in the fact that its jaws are entirely toothless, the skull reminding one quite forcibly of that of a large cursorial bird.

Apparently out of cœlurosaurian stock came an amazing race of giant carnivores, the deinodonts of the late Cretaceous, which in many ways paralleled the megalosaurs yet to be described. The more notable of these were *Gorgosaurus* and *Deinodon*, but especially *Tyrannosaurus* (Fig. 147), the climax of evolution of the great flesh-eating dinosaurs.

Tyrannosaurus reached a length of 47 feet and in bulk must have exceeded the largest of elephants. The massive hind limbs supported the weight of the body and, in a standing position, the animal was 18 to 20 feet high. The head was 4 feet in length, and the powerful jaws bore teeth from 3 to 6 inches long. To this

armament were added the great eagle-like claws of the hind feet and probably of the fore feet, 6 to 8 inches in length. The fore limbs were relatively very small compared with the huge size of the animal but were probably constructed much as in *Allosaurus*, with two or three large curved claws, the inner opposing the others. As the hands could not reach the mouth, it is difficult to conjecture their use other than in combat and possibly in mating.

Carnosauria.—Another group of carnivorous dinosaurs were the megalosaurs which ranged from the Triassic onward. Notable genera are *Anchisaurus* and *Yaleasaurus* known from more or less complete skeletons in the Connecticut Trias. The three most perfect come from the town of Manchester and range in size from perhaps 5 to 8 feet. The hand was large compared with that of later forms and bore five fingers with one large and two smaller grasping claws. These skeletons are preserved at Yale.

Fig. 148.—Restoration of *Allosaurus*, based upon the specimen in the American Museum of Natural History. Length, 34 feet. Jurassic, Wyoming, Colorado, and Maryland.

Zanclodon and *Plateosaurus* were larger Old World forms; out of the latter (Pateosaurus) probably arose not only the later megalosaurs but the amphibious dinosaurs (Sauropoda) as well.

Among other genera are: *Allosaurus* (Fig. 148 and Pl. X), one of the best known of carnivorous dinosaurs, for there is in the American Museum of Natural History a practically complete skeleton mounted in a most lifelike pose. This creature is of great size, being 34 feet 2 inches in length by 8 feet 3 inches high in its present almost horizontal posture. It was collected from Como Bluff, near Medicine Bow, Wyoming, whence came so many of the wonderful dinosaurian and contemporaneous mammalian specimens which the Yale Museum possesses. *Allosaurus* had a comparatively inflexible though deep body and a tail which could undergo little movement as compared with that of a modern lizard or a snake, since its principal use, that of a counterpoise, was best

subserved by its being held out rather stiffly behind. The jaws were loosely hung and could evidently be opened very widely, and there is evidence of some movement of the upper jaw upon the cranium as though the chunks of the prey which the creature tore off were at times of considerable size or possibly the victim was swallowed whole. The teeth are compressed, recurved, and admirably adapted to the owner's implied habits. Both hands and feet were armed with powerful curved claws, doubtless sheathed with talons like those of a huge eagle.

Ceratosaurus, which is known from a single well-preserved skeleton in the United States National Museum, was a contemporary of *Allosaurus*, though not so large. The remarkable thing about *Ceratosaurus*, as the name implies (Gr. κέρας, horn), is the presence of a compressed, horn-like process upon the nose which must have borne a horny sheath. This is one of the extremely rare associations of the possibly defensive horns and carnivorous habits, for among the mammals, and indeed the later dinosaurs as well, it is the herbivores only which are thus endowed.

In Europe and elsewhere than in North America the remains of carnivorous dinosaurs are far less complete, and as a consequence, except for some very well preserved Triassic types, we know but little of them. The generic name of *Megalosaurus*, which gives its title to the group, is applied to most of the later forms from the Jurassic to the final extinction, but doubtless covers as varied an assemblage of larger dinosaurs as lived in the New World.

Sauropoda.—To this group various names have been given. They were called Cetiosauria by Seeley in allusion to their whale-like bulk, and Opisthocœlia by Owen because their neck vertebræ, which have a ball-and-socket articulation, have the concave facet behind and the convex one in front. According to the law of priority this latter term takes precedence over the others, but Professor Marsh's term Sauropoda is the one in most common use.

These creatures were all quadrupedal, although there is reason to believe that when water-borne some may have reared up on the hind feet. Their backbone is a marvel of complexity and has been described in some detail in Chapter XII. The greatest economy of material is manifest in its structure, giving maximum strength with a minimum of bony substance. The limb-bones, on the other hand, are extremely massive, with very rugose ends, as though the joints were formed very largely of cartilage, in sharp contrast with

their bony perfection in the carnivorous forms. This imperfection of the joints in the Sauropoda admits of but one interpretation, a semi-aquatic life, when the weight, largely water-borne, did not subject the ends of the limb-bones to the mechanical impact as it would were the animal wholly terrestrial. A line drawn from shoulder to hip separates the lighter portion of the animal's frame from the weightier as though it represented the water-line. Extreme lightness, especially of the neck, is necessary that it be not unwieldy in the creature's search for food, while weighty limbs were equally necessary to enable their owner to wade into comparatively deep water, for these forms were doubtless more wading than swimming in their habits. In order to support their huge weight, the limbs had become more or less pillar-like, as the straight limb-bones imply, and the sprawling gait of most living reptiles is unthinkable with so ponderous a form. In 1936 footprints of huge Sauropoda have been found in the bed of the Paluxy River, Texas. These deeply impressed tracks show conclusively that the animals walked as the mounted specimens imply. The absence of a tail trace shows that the tail was buoyed up by the water and did not drag on the ground.

The teeth of the Sauropoda are clearly derived from those of carnivores, as they occupy the same place and arise in a similar way. They have, however, lost their sharp point and serrated margins and have become more or less spoon-shaped. As a rule they are large but in *Diplodocus* they are reduced to the size of a lead pencil and are confined to the extreme anterior part of the jaws. Claws also are clearly derived from those of carnivores, as they are laterally compressed, but not so curved, and give no evidence of grasping powers. The foot bore at least three such claws, while the hand evidently possessed but one. The food must have consisted of some abundant and easily obtainable aquatic plants which were probably dislodged by the claws and rake-like teeth and swallowed without mastication. The occasional presence within the ribs of highly polished siliceous pebbles of a material foreign to the matrix in which the specimens were found points to some sort of a muscular gizzard-like structure which, aided by the stones, could reduce the otherwise inert mass of food to a proper condition for subsequent digestion. Such a thing is known in some existing animals, such as certain birds and seals.

Among the notable sauropod genera is *Brontosaurus* (Fig. 149 and Pl. XI), of which the very complete original specimen is preserved at Yale. Another specimen of similar proportions in the American Museum of Natural History measures 66 feet 8 inches long and had an estimated living weight of 38 tons. This speci-

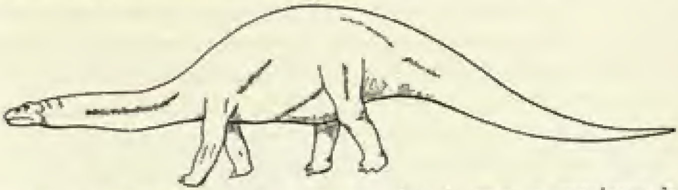

Fig. 149.—Restoration of *Brontosaurus*, based upon a specimen in the American Museum of Natural History. Length, about 67 feet. Jurassic, western North America. (After Lull, from Schuchert's *Historical Geology*.)

men is from the Jurassic near Medicine Bow, Wyoming, and the Yale specimen came from Como Bluff, half a dozen miles away.

Diplodocus (Fig. 150), another well-known sauropod, differs from *Brontosaurus* in the more slender form, so that even with a length of 87 feet it was by no means so weighty as the latter. All of these creatures had most of their length in the extremely slender neck and tail, the body being comparatively short and compact, quite elephantine in fact, especially when viewed in connec-

Fig. 150.—Restoration of the sauropod dinosaur, *Diplodocus*, based upon the mounted specimen in the Carnegie Museum. Length, 87 feet. Jurassic, Wyoming. (After Lull, from Schuchert's *Historical Geology*.)

tion with the limbs. In *Diplodocus* the terminal ten feet of the tail was like a whiplash, as the contained vertebræ did not decrease further in size. This may have proved a very efficient weapon of defense if its use was analogous to that of certain modern lizards in which the tail has much of the effectiveness of a black-snake whip. Aside from this caudal whiplash the Sauropoda were apparently unarmored and weaponless, relying entirely upon their huge bulk

or upon submergence for immunity from attack. An essentially complete skeleton of *Diplodocus* from Sheep Creek, Wyoming, about 15 miles from Bone Cabin quarry, is now mounted in the Carnegie Museum at Pittsburgh.

By far the most gigantic of sauropods has been made known to us in its entirety from Tendaguru, Tanganyika, whence the German expeditions have secured a large amount of material. To this creature the appropriate name of *Gigantosaurus* has been given. If its proportions were those of *Diplodocus*, as the German authorities at first imagined, 120 feet for its total length would not be far from right, but the tail proves to be short, which brings the length

Fig. 151.—Restoration of *Gigantosaurus*, the most ponderous sauropod. Length, about 80 feet. Cretaceous, East Africa. (Modified from Matthew.)

down to 80 feet or more. Matthew therefore regards the creature as somewhat exceeding *Brontosaurus* and *Diplodocus* in total bulk, but distinguished by much longer fore limbs and an immensely long neck—a giraffe-like wader adapted to take refuge in deeper waters, more out of reach of the fierce carnivores of the land. (See Fig. 151.)

Not all Sauropoda, however, were large, for an adult form, *Pleurocœlus*, from the Potomac beds of Maryland, had a total length which did not exceed 12 or 13 feet.

The Sauropoda, judging from their huge bulk, were evidently senile forms, and one would hardly expect their survival over a long period of geologic time, so that while their more conservative relatives, the carnivores, persisted, most of these forms were early

released from the excessive burden of the flesh and suffered racial death early in Cretaceous time, some millions of years before the passing of the dinosaurian dynasty, except for a few, which found asylum in the more remote portions of the earth and apparently survived until toward the close of the Cretaceous. We know of no reason, other than a restriction of their peculiar habitat, for their extinction.

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CHAPTER XXXI

BEAKED DINOSAURS AND ORIGIN OF BIRDS

Ornithischia or Beaked Dinosaurs

The general characters of the Ornithischia, the predentate or beaked dinosaurs, have already been given (see page 467). They were derived in common with the Saurischia from the parasuchian stock, and the Ornithopoda, the more conservative of them, underwent an evolution which very closely paralleled that of the carnivores. Like the Saurischia, they too gave rise to aberrant races, which however did not as with the Sauropoda emphasize bodily bulk so much as arms and armor, and among the later of them were those whose grotesque bizarrerie exceeded that of any known terrestrial forms. None of the Ornithischia was huge compared even with some carnivores, and their bulk was vastly less than that of *Brontosaurus*.

First Record.—The first known record of Ornithischia is that of their fossil tracks upon the Connecticut valley's late Triassic rocks, for with some of the footprints are seen the impressions of smaller hands whose five fingers were armed with rounded claws, like those of known predentates but totally dissimilar to the grasping claws of a carnivore (Fig. 94). And in contemporaneous rocks from far-off Colorado has been found *Nanosaurus* which has been recognized as pertaining to this order. Doubtless the Ornithischia antedated the close of Triassic time, but there is little evidence that their antiquity is as great as that of the Saurischia.

Ornithopoda.—As we have seen from the classification (page 465), three suborders of Ornithischia are recognized. Of these the first is the Ornithopoda, which includes bird-footed forms, unarmored, and bipedal in gait, though unlike the carnivores they occasionally assumed the quadrupedal posture while resting or feeding. Two of the more notable genera are the Connecticut valley *Anomœpus* (see Fig. 94) and *Sauropus*—known only from the footprints and with an estimated length varying from two to eight feet. The Colorado *Nanosaurus* mentioned above is another

small form, as yet imperfectly known. These are all Triassic. Jurassic Ornithopoda are unknown in America until near the end of the period, though they presumably lived in some part of the continent, the absence of a fossil record corresponding to the absence of strata suitable for their preservation.

The late Jurassic (Morrison formation) is characterized by two American genera, *Laosaurus*, a slender type not exceeding six and one-half feet in length, and *Camptosaurus* (Figs. 152; 156,A), several more or less complete skeletons of which are known from Wyoming. The latter are conservative in character and in size, ranging from 7 to 17 feet.

A related form is *Iguanodon* (Figs. 153; 154; 156,B) from Europe, known from no fewer than seventeen remarkably pre-

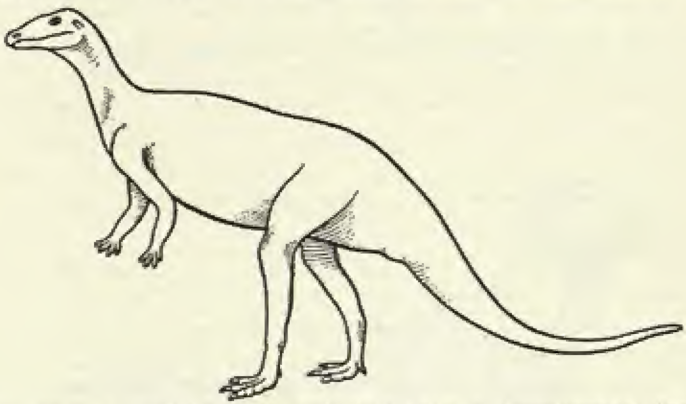

FIG. 152.—Restoration of the predentate dinosaur, *Camptosaurus*. Average length, about 10 feet. Late Jurassic, North America. After Lull, from Schuchert's *Historical Geology*.)

served skeletons found in a coal mine at Bernissart in Belgium. These creatures had evidently fallen into an open fissure in the ancient Carboniferous strata and there, unable to extricate themselves, they died, were buried, and were subsequently preserved together with the remains of other reptiles. Their skeletons, ten of which are mounted erect, the others prone on the rock, are to be seen in the Brussels Museum of Natural History. *Iguanodon* was about 34 feet in length and bore upon the hand by way of weapon a peculiar spike-like thumb. Remains of the genus have also been found on the Isle of Wight, whence it was described by Sir Richard Owen long before the fortunate Belgian discovery.

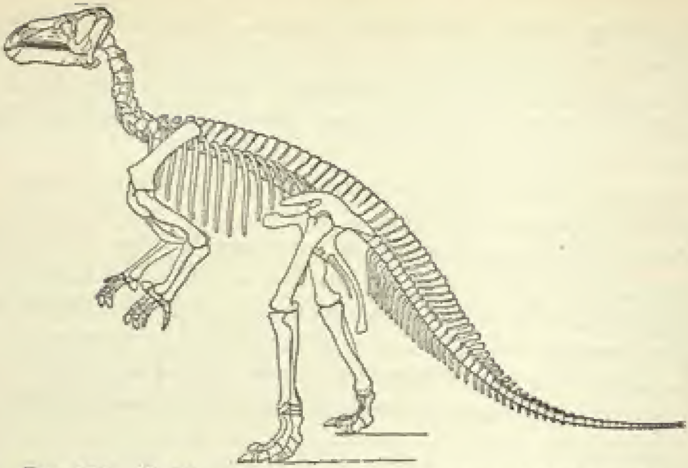

Fig. 153.—Skeleton of *Iguanodon bernissartensis*. (After Marsh.)

Fig. 154.—Restoration of *Iguanodon*. Cretaceous of Belgium and the Isle of Wight. (After Heilmann.)

The English Wealden besides yielding *Iguanodon* has produced a smaller form, *Hypsilophodon*, peculiar in having teeth in the anterior part of the mouth, a characteristic which distinguishes it from every other beaked dinosaur except *Protoceratops* (see page 488) of which our knowledge is sufficiently complete to make a comparison, and in this regard it must be a persistently primitive form. Possibly the Triassic forms also possessed these teeth and this may yet be proved. Both *Camptosaurus* and *Iguanodon* are known from the European Middle Jurassic on.

The Cretaceous of Tendaguru, Tanganyika, whence came the *Gigantosaurus* (see page 476), has also produced an *Iguanodon*-

FIG. 155.—Restoration of *Anatosaurus*, based upon the mounted skeleton in the Yale Peabody Museum. Length, 29 feet. Cretaceous of North America. (After Lull.)

like form, but the details of its structure are not yet announced from Berlin.

Cretaceous time produced several genera of Ornithopoda, which may collectively be called duck-billed dinosaurs from the peculiar character of the mouth, the anterior part of which was often broad as the name implies while the hinder portion of the jaws contained the wonderful dental battery of which we have spoken. No creature of whatever sort is known to have possessed more teeth than *Anatosaurus*, the terminal member of the race.

Anatosaurus (Figs. 155; 156,F; Pl. XII) is the best known genus, as mounted specimens from Wyoming and Montana may be seen at the Yale, American, and United States National Museums. Its length did not exceed 30 feet but it was a fine cursorial type.

It also possessed a powerful tail which, judging from the vertical expansion implied by the bones, was admirably adapted for swimming; for *Anatosaurus* was the contemporary of *Tyrannosaurus* and the swimming tail must have been most effectively used when, hard pressed, it took to the water for safety. Several mummied specimens of *Anatosaurus* have come to light, one of which from Wyoming, preserved in the American Museum, is truly marvellous in the degree of its perfection, for not only is the skeleton entirely articulated except for its hind feet and tail, but the skin, shrunken down on the bones by the heat of the sun immediately after death, is also perfectly preserved, together with traces of muscles and tendons. The skin was utterly without defensive armor, for as now preserved it is very thin and is covered with small tubercle-like scales. The hands, which possessed four fingers, were webbed, as were probably also the feet.

Anatosaurus comes from the close of the Cretaceous, the so-called Lance formation. In rocks of a preceding age, Belly River and Edmonton, there have been discovered some curiously grotesque allied forms, *Saurolophus* with a backward extended crest on the skull, and *Corythosaurus* with a most remarkable helmet-like heightening of the cranium. Both of these are known from articulated specimens collected in the Red Deer region of Alberta, Canada, by Mr. Barnum Brown, who by his discoveries has brought us to a clearer understanding of so many of the formerly ill-known Cretaceous forms. These creatures, however, were not confined to the West, for the New Jersey Cretaceous marl beds have produced *Hadrosaurus*, an ally of *Anatosaurus* and a form which has been known to science for many years (see Fig. 156). Hadrosaurs are also known from Mongolia.

Stegosauria.—The Stegosauria or armored dinosaurs were all quadrupedal, doubtless owing to the great weight of their armament. The armor took the form of high crested plates or spines, or of massive armor plates sometimes welded into a broad cuirass over the hips, evidently the most vulnerable portion of the creature's anatomy. They may well have evolved from the iguanodont-like dinosaurs, developing the armor and consequent modifications of the frame as a defense against their carnivorous enemies. The degree of perfection of the armor in some of the later forms is such as to render them practically invulnerable to any form of animal attack.

The oldest known stegosaurian is *Scelidosaurus* from the English Lias (Lower Jurassic) formation, where the single known specimen was entombed, strangely enough, in marine strata, due probably to its floating carcass having drifted out to sea from some ancient river beside which it lived. As preserved in the British Museum

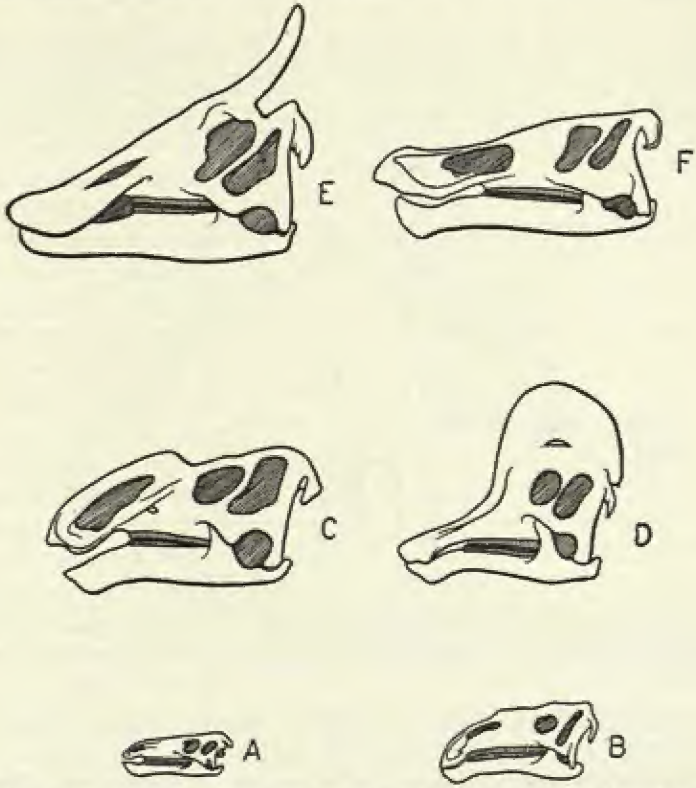

FIG. 156.—Skulls of unarmored predentate dinosaurs. A, *Camptosaurus*, and B, *Iguanodon*, Jurassic and Lower Cretaceous; C, *Kritosaurus*, and D, *Corythosaurus*, Mid-Cretaceous (Belly River); E, *Saurolophus*, late Cretaceous (Edmonton); F, *Anatosaurus*, latest Cretaceous (Lance). All one twenty-fifth natural size. (After Matthew.)

of Natural History, *Scelidosaurus* is only $12\frac{1}{2}$ feet long and its armor consists of two rows of oval bony scutes each with a low fore-and-aft keel not unlike similar elements in a modern crocodile. In addition to these there are a pair of large spines on the shoulders. In late Jurassic and early Cretaceous (Wealden) time we have

recorded several armored dinosaurs in England and the adjacent continent, known as *Polacanthus* and *Omosaurus*. Of these the former is small, not over 12 feet in length by 3 in height, with a broad rump-shield formed of coalesced plates, and sundry spine-like plates which have been arranged by the restorer in two rows along the neck, back, and tail. Their precise position, however, is not assured. *Omosaurus* is another heavily armored form, some species of which were very large; it is as yet incompletely known.

Stegosaurus (Figs. 157; 158; Pl. XIII) was a late Jurassic type, but in spite of the fact that it has given its name to the group of

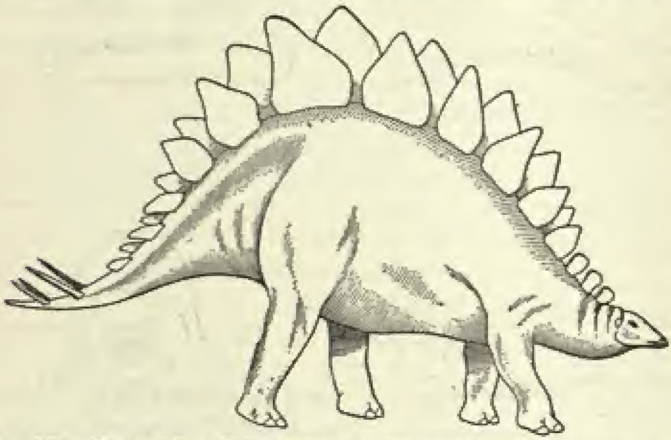

Fig. 157.—Restoration of the armored dinosaur, *Stegosaurus*, based upon the mounted skeleton in the Yale Peabody Museum. Length, about 20 feet. Jurassic, Wyoming and Colorado. (After Lull, from Schuchert's *Historical Geology*.)

armored dinosaurs, it was not typical, being a highly spinescent senile side branch which died out without issue. In many ways this was the most grotesque of dinosaurs, an awkward angular brute, very high at the rump and low at the withers, with the back ornamented by two rows of huge upstanding plates and the end of the tail armed with fearful horn-like spines 25 inches or more in length. The huge plates which ran along the back culminated in the ones over the pelvis or the base of the tail, beyond which they diminished. A study of the skeleton mounted at Yale and another articulated specimen at Washington betrays great muscular power especially in the tail and hind limbs. The inference is therefore that the plates served for passive, the spines for active

defense, possibly offense. But the nervous system of *Stegosaurus* is the most remarkable feature, for its brain was very diminutive, the entire cranial cavity having a volume of but 56 c.c. Thus the estimated weight of the brain could not have exceeded two and one-half ounces, while the total weight of the animal must have been greater than that of the largest of living elephants whose brain averages at least 8 pounds and may run to nearly 11, 80 times that of the dinosaur. In comparing the relative potential intelligence of the two, one has also to bear in mind the great preponderance of the cerebrum, the seat of intellect, over the other parts of the elephantine brain, while in *Stegosaurus* the cerebrum constituted hardly more than a third of the entire brain weight. Or, as Professor Williston has expressed it, the seat of a stegosaur's intelligence is no greater in volume than that of a three-weeks-old kitten! In contrast with the diminutive brain-case, however, the neural canal in the sacrum is of startling dimensions, for a cast thereof displaces no less than 1200 c.c. of water, thus giving it a mass more than twenty times that of the brain. This was the seat of the reflex and coördinating control of the huge hind limb and caudal muscles and is further evidence of their very frequent and effective use. The life of *Stegosaurus* was not psychological, but essentially physiological—an animated, largely automatic machine!

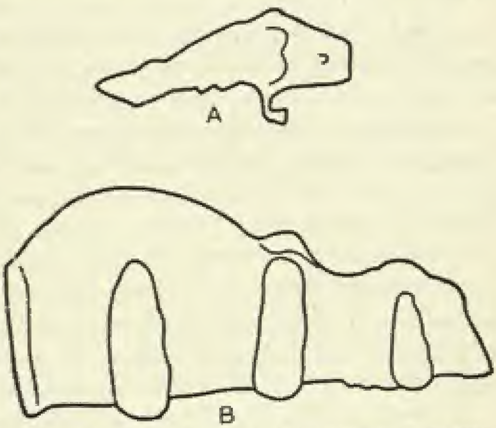

FIG. 158.—Brain space (A) and sacral enlargement (B) of the spinal canal of *Stegosaurus*. Drawn to scale, one-fourth natural size. (After Lull.)

The Cretaceous rocks of North America have produced other more conservative armored dinosaurs, *Nodosaurus*, *Ankylosaurus*, and *Palæoscincus*, of which the last is the best known. *Ankylosaurus* was a contemporary of *Tyrannosaurus* and the duck-billed dinosaurs, and was not unlike a huge horned toad. The head was broadly triangular with a horny beak and very feeble teeth, while

the trunk was covered with a veritable cuirass of keeled and spined plates which formed an invulnerable armor. The tail was also enclosed in a bony sheath which probably bore spines, like the battle-mace of a mediæval knight, and was the offensive weapon. Even *Tyrannosaurus* could not effectively attack one of these creatures when it settled down and tucked in its short legs beneath its body.

Ankylosaurus was a remarkable reptilian prototype of the armored mammalian glyptodonts of the Pleistocene, the similarity even extending to a club-like fusion of armor on the tail, especially in the genus *Dœdicurus*. In *Dœdicurus'* day it was the great saber-tooth cat, *Smilodon*, against whose attacks the creature may have guarded itself in much the same way as the ankylosaur met those of *Tyrannosaurus* (see Chapter XXXVIII).

Ceratopsia.—The horned dinosaurs, or Ceratopsia, are, except for Mongolia, largely North American, and more than that, their remains come almost entirely from the eastern uplift of the Rocky Mountain region from Alberta to New Mexico. That they lived only within these narrow limits, however, is hardly to be supposed. Their geologic range is also brief in extent, as they are confined exclusively to the Upper Cretaceous period. The degree of their evolution when they first appear is, however, indicative of an origin not later than the lower Cretaceous.

Triceratops (Figs. 159,C; 160) is a late Cretaceous member of the group, but is the best known and may be taken as typical. It was a huge creature of rhinocerine aspect, from 20 to 25 feet in length, of which from one-quarter to one-third consisted of the great head, for whereas in all other dinosaurs the head is small, here the reverse is true. This is due partly to the great expansion of the cranial roof for the support of the horns, but particularly to the backward extension of the rear of the skull into a widely expanded frill or crest for the protection of the neck, and also for the attachment of the powerful muscles of the back of the neck, giving this group of animals tremendous prowess, correlated with their armament and the great bulk and power of the enemies which they were called upon to withstand. One *Triceratops* skull in the Yale collection measures 8 feet 4 inches over-all, and that of the allied *Torosaurus* 8 feet 7 inches, making the latter the largest known skull of a land animal.

The skeleton of *Triceratops* gives evidence of enormous strength,

especially in the great fore limbs and shoulders. But the armament was the most striking thing, for the mouth was armed anteriorly with a sharp cutting beak like that of a turtle, and the nose and portion of the skull above the eyes bore huge horns, three in number, hence the name *Triceratops* (three-horned face). In the earliest American forms the nasal horn was always the dominant one, straight or curved either forward or backward, while the frontal horns above the eyes ranged from mere rudiments to fairly well developed organs. The principal Belly River genera

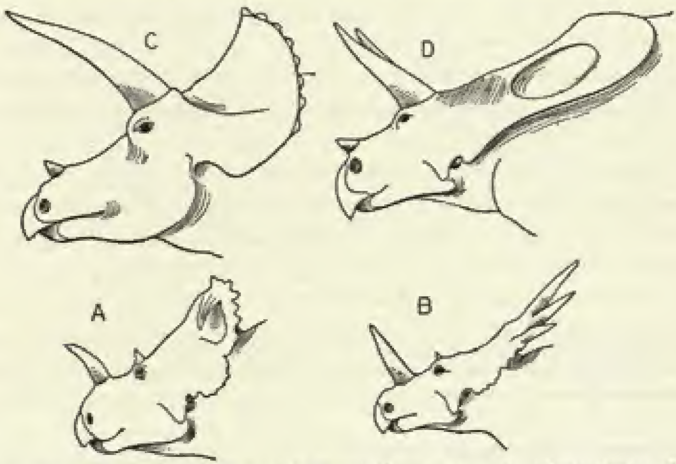

FIG. 159.—Heads of horned dinosaurs, Ceratopsia. A, *Monoclonius*, Upper Cretaceous (Belly River); B, *Styracosaurus*, Belly River; C, *Triceratops*, uppermost Cretaceous (Lance); and D, *Torosaurus*, Lance. Drawn to scale. *Torosaurus* skull 8½ feet long. (After Lull, from Schuchert's *Historical Geology*.)

were *Monoclonius* (Fig. 159,A) and *Ceratops*. Another was *Styracosaurus* (Fig. 159,B), which was remarkably spinescent, having a huge straight nasal horn and at least eight more horn-like processes around the margin of the frill. The crest in all of these earlier types was incomplete in that it was penetrated by two large apertures, one on either side. In the latest Lance forms the frontal horns were predominant, and were very long in the later types, while the nasal tended to reduce, becoming entirely obsolete in one genus, *Diceratops*. *Triceratops* and *Diceratops* both had a completely bony frill with no trace of the ancestral apertures. In *Torosaurus* (Fig. 159,D), on the other hand, while the horns were like those of *Triceratops*, the two apertures still persisted in the immensely expanded

crest. That these horns and the defensive frill were put to actual use is highly evident, for broken and healed horns, broken jaws, and punctured crests are not unusual with these skulls. And these are the deep and grievous wounds, doubtless few compared with the many superficial injuries which the creatures must have suffered in the combats of rival males or in defense against their arch enemy, the tyrant saurian. The Mongolian *Protoceratops*, at least structurally ancestral, possessed the bony frill but was hornless. This animal laid some of the dinosaur eggs found by the Andrews

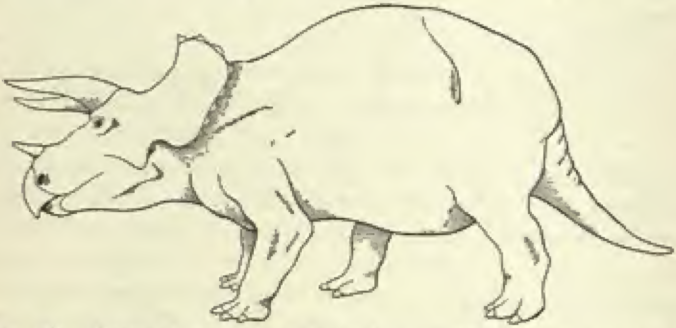

FIG. 160.—Restoration of the horned dinosaur *Triceratops*. Length 20–25 feet. Upper Cretaceous (Lance), western North America. (After Lull, from Schuchert's *Historical Geology*.)

Expedition to Mongolia, and not only were the eggs found, but 72 skulls representing the entire ontogeny from the unhatched young to the full-grown animal, which is believed to be without parallel in vertebrate paleontology.

Summary

As in the history of nations the members of various human races intermingle, so the dinosaurs are interwoven not alone with the various types of their own stock, but with the other kinds of animals and plants which together with physical conditions go to make up the environing complex. A summary of the changing life conditions with their influence on the successive dinosaurian societies is necessary to an understanding of their evolution.

The first relics of dinosaurian life are found in the early Mesozoic (Mid-Triassic) rocks of Central Europe, though as they appear shortly after in those of North America one is led to infer that the initial evolution occurred in what may have been an annectant

land mass lying across the North Atlantic. Ancestrally, the dinosaurs were quadrupeds remotely related to the crocodiles; but the increasing aridity of climate, clearly indicated by the character of the geologic sediments, placed a high premium on ability to travel rapidly and far in search of food and drink, and may well have been the impelling force that raised these creatures erect from the prone gait and posture of their progenitors and stimulated their rapid evolution into the several types.

The so-called continental rocks include such as are formed by stream-borne and lake-borne sediment or by sands and volcanic ash carried by the winds. In contrast to marine deposits these are extremely scarce, and yet they alone, with rare exceptions, contain the remains of terrestrial animals. We are given, however, aside from scattered records, three or four vivid pictures of the environment, both physical and organic, wherein the dinosaurs dwelt. Fortunately for us these glimpses are given in the early stages, in the middle, and at the close of the dinosaurian career, showing the race in the period of its youth, its full maturity, and in its extreme old age.

Triassic.—The first of these pictures is of great interest, for the scene is laid in what is now the Connecticut valley; the time, late Triassic. Here one must imagine a broad valley rimmed by environing uplands of older rocks, in its climate and sparse vegetation similar to the conditions to be seen to-day by the traveler through the semi-arid regions of the great Southwest. The plant life is somber: huge scouring rushes, ferns, and pines, with no flowering plant to break the monotony of the dull dust-covered greens. Here and there are dry stream-beds carrying at times great floods, while occasionally there are formed extensive bodies of water with characteristic insects and other invertebrates, fishes, and crocodile-like reptiles. In the Connecticut valley deposits, skeletons are extremely rare and the few which have been found are largely those of dinosaurs, and in but three or four localities. The footprints, however, for which this region is justly famous, are numberless, and indicate hosts of creatures of more than a hundred kinds, as full a record of vertebrate life as in any other time and place in the geologic past. The dinosaurs are mainly carnivorous, though impressions of the feet of herbivores give indubitable evidence of their presence at this time.

Jurassic.—During the long Jurassic period, the second division of the reptilian age, the known fossil-bearing rocks are so largely

of marine origin that, except for rare instances where the animal has accidentally been carried into the sea, the record of terrestrial life is almost a blank. At the close of the Jurassic, however, we have another glimpse of well-nigh the entire assemblage of dinosaurian life. The scenes are laid along the eastern United States from Maryland southward, but more notably in Wyoming, Colorado, and Utah, and in the Old World in southern England and northern France and Belgium. In contrast with the aridity of the former scene the climate is now moist, and the eye ranges over an extensive, low-lying country with misty bayous in which the huge Sauropoda, now in the flower of their evolution, find retreat. In Europe and western America the vegetation, though far more luxuriant, is of the same monotonous type as that of the Trias; but in central and eastern America appear representatives of the flowering plants, the dominant flora of to-day. Here are predentate dinosaurs, armored and unarmored, and while the former are still relatively few, *Stegosaurus* already shows the senile grotesqueness which heralds its extinction. Carnivores small and large, now in their millennium of numbers and differentiation, ceaselessly seek their prey.

Late Cretaceous time ushers in the third and last scene, of much the same geographic extent as before, but with the sharp contrast of an essentially modernized flora, for the forests now contain many familiar trees and plants though often in unfamiliar combinations. Again our record is of low-lying country—stretches of everglade and swamp lands with higher areas between—but the denizens have changed; for while the carnivores are now in their maximum of size, the Sauropoda have run their course and, except for a few remote survivors, are largely extinct. Unarmored dinosaurs are in their prime, only in rare cases showing indications of degeneracy, while the relatively few heavily armored types are represented by the most impregnable of their race. The horned dinosaurs begin and end their brief evolutionary career.

Thus it will be seen that the law of the balance of nature was as operative during the Mesozoic as it is to-day, and that as the carnivores grew and waxed mighty, the herbivores were forced to meet the menace of their aggression in several ways; either by increase in numbers, for the remains of carnivores are very rare compared with those of the herbivorous orders, or by speed, or by increase of bulk, which also meant a partial forsaking of the ter-

restrial habitat as with the Sauropoda and Hadrosauridæ. Or it meant the development of armament, either of defensive armor as in the stegosaurs, or of aggressive armor and weapons as in the ceratopsians. The lack of brain power placed a premium upon brutality, and never, perhaps, before nor since has the animal world felt to so great an extent the burden of preparedness.

Extinction.—One of the most inexplicable of events is the dramatic extinction of this mighty race, for in the rocks of undoubted Tertiary age not a single trace of them remains. One student has argued internecine warfare amongst the dinosaurs themselves; another, the destructive slaughter, not of adults but of the young, possibly while yet in the egg, by small bloodthirsty mammals; yet another, change of climate, either by the diminution of the necessary heat without which no reptilian race may thrive, or of the moisture with an accompanying change of vegetation. These are all conjectural causes of extinction; but this we know, that with the extensive changes in the elevation of land areas which marked the close of the Mesozoic came the draining of the great inland Cretaceous seas along the low-lying shores of which the known dinosaurs had their home, and with the consequent restriction of old haunts came the blotting out of a heroic race. Their career was not a brief one, for the duration of their recorded evolution was thrice that of the entire mammalian age. They do not represent a futile attempt on the part of nature to people the world with creatures of insignificant moment, but are comparable in majestic rise, slow culmination, and dramatic fall to the greatest nations of antiquity.

Origin of Birds

Birds are doubtless derived from the same stock as gave rise to the dinosaurs, the Pseudosuchia, and Huxley years ago recognized the very close reptilian affinities of the birds by calling them "glorified reptiles."

Avian Distinctions.—The principal points of contrast between birds and the reptilian dinosaurs of the more generalized type lie not in the character of the pelvis or of the foot, nor in the presence of ossified tendons along the vertebral column, nor in the presence of teeth, for these are all likenesses, and only a few out of many such. The main distinctions are due almost without exception to the assumption on the part of the bird of aërial life, and

hence the birds may be considered simply the volant branch of a group of which the dinosaurs were the terrestrial members.

As a result of their flying adaptation, birds have the fore limbs transformed into wings, and the scales, except for those on the feet, altered into feathers for warmth and to increase the supporting surface. The blood becomes warm, with an adaptation to maintain it at a given temperature, which may, however, have been true possibly to a limited extent of the dinosaurs. The birds also have developed pneumaticity of the skeleton for lightness as in the cœlurosaurs and an extensive system of air cells throughout the body. Their organs of nutrition are highly developed because of the great expenditure of energy which flight necessitates, and their circulation is very perfect, which again may have been true of dinosaurs, but this we have no means of knowing. The loss of teeth is foreshadowed in the dinosaurs, the dental battery of several being a very inadequate thing, not so efficient in fact as that of the Cretaceous birds, while in *Struthiomimus* teeth were entirely lacking.

Origin of Flight

Several hypotheses have been advanced to account for the origin of flight, one group of authorities postulating an antecedent

FIG. 161.—Restoration of a hypothetical proavis, or ancestor of the birds. (After Nopcsa.)

arboreal life, while others would derive flying forms from those of cursorial habits, and yet others have believed that the birds are diphyletic, the carinate or flying birds having an arboreal ancestry while the ratite or cursorial birds were of terrestrial stock.

Cursorial origin of flight has been advocated mainly by the Hungarian paleontologist, Francis Baron Nopcsa. A discussion

of his theory follows. Nopcsa did not believe that the flight of bats and pterodactyls, which fly by means of patagia, and birds, which fly by means of feathers, could possibly have arisen in the same way, for the patagium-flier must always adapt both fore and hind limbs and tail to the support of the membrane, whereas in a generalized feathered animal only the feather-supporting elements need become affected by volant specialization. The development of the posterior limb in such an animal is but little if at all affected by the development of flight. The hind limbs of birds are so similar in structure to those of the cursorial dinosaurs, in which so far as we know no flying powers were ever developed, that the type of modification which they both represent can only be interpreted in the light of a function possessed by each.

The inference is therefore that birds arose from bipedal long-tailed cursorial reptiles which, during running, oared along in the air by flapping their free anterior extremities. These would of course be more effective if their breadth could in some way be increased to give them a greater bearing surface, and the increasing size of the scales along the arm margin would be a ready means to this end. Similar scales might develop along the margins of the tail for the same reason that lateral hairs have developed on the tail of certain bipedal mammals (jerboa, see Fig. 48). These scales would extend, lighten, and ultimately evolve into feathers which would not only subserve the function of flight but, acting as clothing, retain and aid in the increase of temperature, which in turn would help to improve both the physical and mental activity of these forms; and this is a sufficient reason for the dominance of the birds over all other aërial rivals and for their survival after the extinction of their dinosaurian kindred.

A Danish scientist, Gerard Heilmann, who has made an exhaustive study of bird origin, does not accept Nopcsa's theory, for with purely cursorial animals the grasping hind toe or hallux tends to vanish and the fore limbs to reduce in size rather than elongate. He believes, on the contrary, that the birds and certain dinosaurs come from a common arboreal stock, from which the latter early returned to a terrestrial mode of life. On the part of birds the return was long delayed until after the assumption of flight.

The pro-avian was therefore a form intermediate in structure between certain Pseudosuchia, such as the Triassic *Ornithosuchus*, and the Jurassic *Archæornis* (*Archæopteryx* in part), the earliest

known bird. It had grasping feet which were in no way concerned with flight as with bats and pterodactyls, a hand with three long, slender fingers, and an elongated reptilian tail. In some of the pseudosuchians the scales are already elongating and show striæ indicative of the way in which feathers arose, for the feather may be considered as a long, frayed-out scale. Heilmann thinks that the feathers first evolved as a heat-retaining clothing, from which their supporting function along the margins of the fore limb and tail could readily be derived by further elongation. The pro-avians used arms and tail for support in their soaring leaps from tree to tree or to the earth, for it is conceivable that, while good climbers, they were also well able to run on the ground, in contrast to the helplessness of bat or pterosaur under like conditions. In either situation, in contrast to their sluggish reptilian forebears, the birds were always active animals in the pursuit of their prey, which not only stimulated the evolution of warm blood and of flight but made them dominant forms in their true environment, the air.

Geologic Record

Upper Jurassic.—The earliest recorded birds are known from two well-preserved specimens, one headless, now in the British Museum in London, (*Archæopteryx*) the other, which bears a head, in Berlin (*Archæornis*). They are both from the lithographic quarry at Solenhofen, Bavaria, and were contemporaries with *Compsognathus*, not, as we have seen, the earliest, but the smallest known dinosaur.

Archæornis was about the size of a crow, feathered, and with fair powers of flight. There were, however, several characteristics wherein it was more reptile-like than are modern birds. These are the presence of teeth in both jaws, the free, clawed fingers of the hand which were not yet fused into the form of the modern wing, the feebly developed sternum, and especially the possession of a long tail on either side of which the rectrices or steering feathers were arranged. In all subsequent birds the tail is shortened and the feathers are disposed fan-wise (see Fig. 80,A; and Pl. XIV).

Cretaceous.—The Cretaceous chalk (Niobrara) of Kansas has produced the next recorded avian remains in geologic time. These strata are marine, for besides invertebrates and sharks and other sea-fishes, they contain mosasaurs, sea-turtles, plesiosaurs, and the fish-eating pterodactyls *Nyctosaurus* and *Pteranodon*. The birds

belong to two main sorts, both of which were doubtless aquatic, but the larger of them, *Hesperornis* (Pl. XV), was especially so, since it had lost the power of flight. The other, *Ichthyornis*, was a small tern- or gull-like bird well endowed with flying powers and essentially modern except that, like *Hesperornis*, its jaws still bore teeth. It is interesting to note, however, that in common with the predentate dinosaurs (except one or two) the teeth in both of these genera were confined to the maxillary and dentary bones, the pre-maxillary, which forms the forward part of the upper jaw, being toothless.

Hesperornis was a splendid bird measuring over four and one-half feet in length, with powerful hind limbs which, while rendering the bird awkward on land, must have been very adequate swimming organs. Loss of flight is indicated by the reduction of the shoulder-girdle, and especially of the wing, which is represented by a long, slender humerus, the fore arm and hand being entirely lacking. The breast-bone also is devoid of a keel for muscular attachment, resembling that of an ostrich. On the whole, *Hesperornis* finds its recent analogy in the loons or great divers, and except for its flightless condition may have had quite similar habits of life. Other Cretaceous genera are known, though very imperfectly, but, with one possible exception, they all agreed in the possession of teeth, although in other respects they were essentially modernized. Two original mounted skeletons of *Hesperornis* and two of *Ichthyornis*, the latter unique, are preserved at Yale.

FIG. 162.—*Diatryma*, a giant Eocene bird, contemporary with the four-toed horse Height about 7 feet. (Restoration after Matthew.)

Tertiary birds leave but little to the imagination, as they are similar to those of to-day. It is interesting to note, however, that the loss of flight occurred apparently several times among Tertiary

forms, for even from the Eocene formation in most parts of the world numerous big Ratites (*i. e.*, cursorial birds), such as *Diatryma* (see Fig. 162), are known, which can only have originated from badly-flying ground-birds, whereas in more modern times the Ratites are apparently vanishing from the earth's surface.

The birds as a class are a very compact group and do not begin to show the range of size and adaptation of the reptiles as a whole; in fact, in this respect they hardly rank with the dinosaurs. With them it is perfection and multiplication of detail, and the most essentially modern among them are the small tree or perching birds of the order Passeres.

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CHAPTER XXXII

ORIGIN OF MAMMALS AND RISE OF ARCHAIC MAMMALS

Definition of Mammals.—Mammals may be defined as warm-blooded creatures whose body is more or less clothed with hair, whose young are produced alive, except in the egg-laying monotremes, and are nourished for a while after birth by the secretions of milk (mammary) glands. The skeleton shows several important distinctions from most reptiles and birds, having a double occipital condyle—the articular facets which unite the skull with the first cervical vertebra—and having a simple lower jaw. In reptiles and birds, on the other hand, the condyle is generally single and the jaw is a bony complex. There is also an intervening bone, the quadrate, between the jaw and the skull, which is lacking in the mammal. A further mammalian distinction lies in the fact that the vertebræ and limb-bones ossify[1] from three separate bone-forming centers: the body or shaft, as the case may be, and the articular ends or epiphyses. The mammalian dentition is peculiar in the local differentiation of the teeth (heterodonty) into incisors, canines, premolars, and molars, and also in that there are but two sets in series, the milk or lacteal teeth and the permanent ones; never does one see anything comparable to the amazing successional teeth of the predentate dinosaurs, for instance. Secondarily acquired simplicity of the teeth may occur as in the toothed whales, and the number of teeth may be increased or reduced.

The mammals are certainly the highest class of vertebrates from many standpoints; in some ways, however, this place may be disputed by the birds, but the latter represent the culmination of one line of ascent and the mammals another.

Origin of Mammals

Stock.—At least two views have been held as to the origin of mammals. The older one, that advocated by Huxley in 1880, would

[1] All bone consists first of cartilage, the actual bony material, lime phosphate, etc., being formed therein in a definite way by the activity of certain cells, the bone corpuscles. This is known as ossification.

derive them from the Amphibia. Much in Huxley's theory is undoubtedly correct, except that authorities do not now believe that the Amphibia represent the *next* lower stage, but that there was an intervening condition, one in which gill-breathing had been lost but truly mammalian characters had not yet appeared, although some of them were already foreshadowed.

There are found in Triassic rocks in South Africa a group of reptiles known as the Cynodontia, in allusion to their dog-like teeth, and there seems to be a large body of evidence in favor of the view that out of this group, although from no known member of it, the mammals have been derived (see Fig. 163). The cynodonts resemble the mammals in the possession of a heterodont dentition, in that the teeth are clearly divisible into incisors, canines, and molars, and in the paired occipital condyles, in addition to which there are similarities of construction. Structurally the cynodonts bridge the gap between reptiles and mammals because while the dentary, the single bone of the mammalian lower jaw, is large and important, the jaw is nevertheless complex in that it possesses the several bones typical of the reptile. There are other reptilian characters as well, all of which may reasonably be expected in the remote ancestors of the Mammalia. These cynodont reptiles are low in the reptilian scale, far removed from the dinosaurs and birds with which we have been concerned, although capable of as high a degree of specialization along other lines.

FIG. 163.—Skull of cynodont reptile, *Nythosaurus larvatus*, Trias, South Africa. Note the mammal-like tooth differentiation, but complex reptilian jaw. *Ang*, angular; *Art*, articular; *Dent*, dentary; *Ju*, jugal; L, lachrymal; *Mx*, maxillary; *Na*, nasal; *Pa*, parietal; *Pmx*. premaxillary; *PoO*, postorbital; *Pr. F.*, prefrontal; *S. Ang*, surangular; *Sq*, squamosal. (After Broom, from Schuchert's *Historical Geology*.)

Place of Origin.—While we find members of this order in both North America and Africa, although they must have been much more widely diffused, it was possibly in the latter place that the mammals arose, probably due not so much to the potentiality possessed by the reptiles of one place over the other as to a happy combination in Africa of a potent stock and an impelling cause.

Cause.—A cause for the origin of the mammals has been mentioned in Chapter XIX under the caption "Significance of cursorial adaptation." Therein is emphasized the statement made by Broom that all of the characters wherein a mammal differs from a reptile are the result of increased activity, for he says that when the cynodont took to walking with feet underneath and body off the ground, it first became possible for it to become a warm-blooded animal. But back of this lay impelling geologic causes which Broom does not even hint at. These were, first, increasing aridity of climate, which from Permian time well into the Jurassic seems to have been characteristic of all lands, as the extensive series of red sediments may imply. And aridity has been found to be a great stimulative to speed. Add to this the evidence, especially in the southern hemisphere between latitudes 20° and 35°, of extensive glaciation—greater even than in the more familiar Pleistocene Glacial period—and we have a high incentive to the retention of bodily heat. For it is well known that cold more than any other factor limits the activity of reptiles and effectively prevents their distribution into the higher latitudes. For a while, perhaps, there were recurring warm seasons, sufficiently long and frequent so that a normal reptilian life could still be led, the creature hibernating when the weather became too severe. But, as in the case of the æstivating lung-breathing fishes, sufficient time must still be had for the active portion of the creature's career, so that, although in the origin of terrestrial forms premium would be placed upon the capability of atmospheric respiration, here it would be upon ability to withstand the cold and yet remain active, and the acquisition of warm blood and a heat-retentive clothing is the only possible means to this end. Hence as immediate geologic causes of mammalian evolution we have, first, aridity, the incentive for speed, rendering *possible* the development of warm blood, and second, the increasing cold to place a premium upon such as did develop it and to eliminate those which did not.

Time.—The time of mammalian evolution can only be fixed within certain limits. Geological evidence, if we have read the cause aright, points to its inception in Permian time for "there is now undeniable evidence that in middle Permian times most of the lands in the southern hemisphere were subjected to as severe a glacial climate as that of the present polar areas, and that this Permian glaciation was likewise interrupted by times of warmth" (Schuchert).

On the other hand, the geologic record seems to point to the Triassic at any rate as the time of the *culmination* of the evolutionary movement, for here are found for the first time the cynodont reptiles and the actual relics of the mammals themselves. But the cause must always precede the effect and it may be that the known cynodonts were persistent reptilian survivors of the group out of which the mammals actually sprang, and that the earliest known mammals themselves had already had a long transitional period. It seems reasonable to suppose, therefore, that the time of mammalian origin was not later than Middle Triassic nor earlier than Lower Permian.

Mesozoic Mammals

Deployment.—As with the dinosaurs three important vistas are open to our scientific vision, so it is with the Mesozoic mammals. We see them in late Triassic time in Germany, England, and South Africa, in Jurassic in eastern Wyoming, and in late Cretaceous in the same general region. Again as in the dinosaurs, there are other occurrences of less importance, but the three mentioned above are so placed in time that their interest is thereby greatly increased, for they may be considered roughly to mark the stage of evolution of this all-important class at the close of each of the three great periods of the Mesozoic—the Triassic, the Jurassic, and the Cretaceous.

General Characteristics.—The general characteristics of Mesozoic mammals are, first, their small size, for the average among them could hardly have exceeded the stature of a rat, although some attained that of a fox terrier. Their habits were doubtless varied. Some had sharp-pointed teeth comparable to those of living insectivores (see Fig. 167), and like them adapted to a varied animal diet—insects, worms, young birds, and reptiles—in other words, such creatures as they overcame, for in all probability the gratification of their appetite was limited largely by their lack of prowess. Others had teeth better fitted for an herbivorous than an animal diet, with sharp cutting incisors, almost like those of a rodent in front, shearing premolars and many-cusped (multituberculate), broad-crowned, grinding teeth behind (see Fig. 166). In certain instances their teeth are quite suggestive in general form of those of the rat-kangaroos of Australia and Tasmania, all of which are small animals, hardly exceeding a rabbit in size, noc-

turnal, and feeding on the leaves of various kinds of grasses and other plants as well as roots and bulbs which they dig up with their fore-paws. There is little doubt of the herbivorous character of these Mesozoic forms, although in trying to fix upon a precise dietary from analogy the possibilities of the contemporaneous vegetation must always be borne in mind.

Habitat.—Matthew has discussed in some detail the implied habitat of the Mesozoic mammals and has come to the conclusion that they were largely arboreal, his conviction being based chiefly upon the skeletal characteristics displayed by their descendants. He says: "The Cretaceous ancestors of the Tertiary mammals were small arboreal animals of very uniform skeletal characters, but probably somewhat differentiated in dentition according as fruit, seeds and nuts, or insects formed the staple of their diet. At the beginning of the Mesozoic the available modes of life for land vertebrates were chiefly the amphibious-aquatic, the arboreal, and the aërial, the terrestrial habitat being subordinate because the upland flora was largely undeveloped or inedible as compared with its present condition. The three available provinces were occupied by reptiles, mammals, and birds respectively. In the later Cretaceous the spread of a great and varied upland flora vastly extended the terrestrial province, and opened a new and constantly widening field for the expansion of the Mammalia. . . . The little that is known of the Mesozoic Mammalia fits in with our hypothesis of their arboreal habitat but adds little to the evidence in its favor. Practically nothing is known of their skeletal structure; they are all of small or minute size, with teeth of insectivorous or granivorous type. . . . Their minute size, and association, in strata of fresh or brackish water origin, with large amphibious and aquatic reptiles and with abundance of fossil wood, suggest that the deposits in which they occur were laid down in extensive forest-clad river deltas and coastal swamps, and that the minute Mammalia represent the arboreal fauna of these forests."

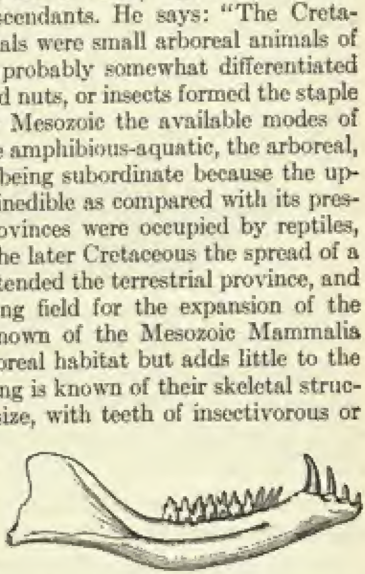


FIG. 164.—Cynodont reptile, *Dromatherium sylvestre*, Trias, North Carolina. Twice natural size. (After Osborn, from Schuchert's *Historical Geology*.)

Classification.—The order "Protodonta," which apparently has no validity, included two small jaws called respectively *Microconodon* and *Dromatherium*. They were discovered in a coal mine at Egypt, North Carolina, and are of Upper Triassic age, contemporaneous with the far-famed Connecticut valley beds. The dentition is that of the cynodont reptiles rather than mammalian, and the principal evidence of mammalian affinity lies in the apparently simple jaw, which, as preserved, consists of but a single

bone (see Fig. 164). Recent restudy by Dr. George G. Simpson has shown, however, that the specimens are defective and that, in all probability, the jaw was complex. This necessitates their reference to the cynodont reptiles rather than to the mammalian class.

In the order *Triconodonta*, the teeth are more perfectly formed, but the molars are characterized by having but three cusps arranged in a single longitudinal row; of these the middle cusp is usually dominant, the others being much smaller. At times, however, the latter may equal the median cusp in height. Their relationships are doubtful.

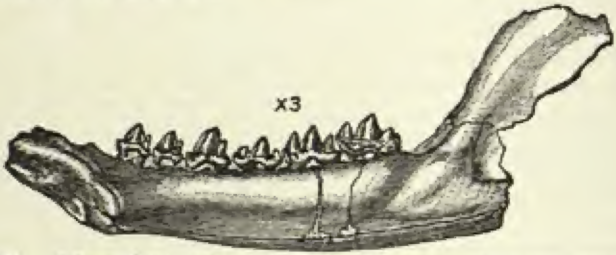


Fig. 165.—Triconodont mammal, *Priacodon ferox*, *Jurassic*, Wyoming. Three times natural size. (After Marsh.)

Triconodonts first appear in the Lower Jurassic (Stonesfield slate) of England, in the genus *Amphilestes*. *Triconodon* itself comes from the Upper Jurassic of England, while a related, possibly equivalent genus comes from the Jurassic of Como Bluff, Wyoming, which is the upper limit of their range.

The *Allotheria* or Multituberculata are among the oldest of mammals, for their characteristic molar teeth are found in Upper Triassic rocks of Germany and they range into Lower Eocene time. Geographically they are very widespread, as they have been reported from Europe, Asia, and Africa and from North America. Little is known of the skeleton, but jaws and teeth are more or less abundant and several skulls (see Fig. 166) have been found. They had a single pair of rodent-like incisors above and below, while the molars bore two or three longitudinal rows of tubercles, hence the name Multituberculata; the premolars were either simple-cusped or compressed, sharp-edged, cutting teeth.

Fig. 166.—Multituberculate mammal (allothere), *Ptilodus gracilis*, Paleocene (Ft. Union), Wyoming. About natural size. (After Gidley, from Scott.)

The most notable forms are *Tritylodon*, a large type from the Karroo beds (Lower Jurassic) of South Africa; *Thomasia* of the Upper Trias of Europe; *Plagiaulax* from the Jurassic of Europe and North America; *Ptilodus* (Fig. 166) and *Tæniolabis* from the Paleocene of North America. The Allotheria have been included under the Marsupialia, but there is not the least likelihood that any existing mammals were derived from them.

The *Symmetrodonta* are a little-known group confined to the Upper Jurassic of England and North America. Their molars have three main cusps arranged in a triangle. *Spalacotherium* from England and *Tinodon* in North America are the best known representatives. They were apparently an isolated order, distantly related to the Pantotheria.

In the next order, the *Pantotheria*, the dentition, while simpler, suggests that of the insectivores to such an extent that they have

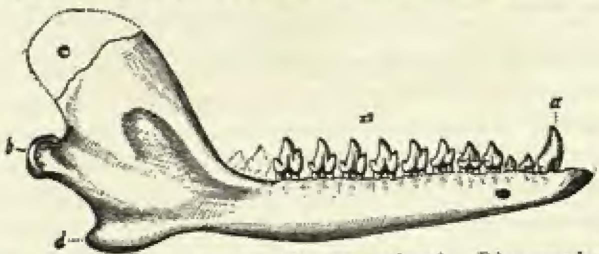
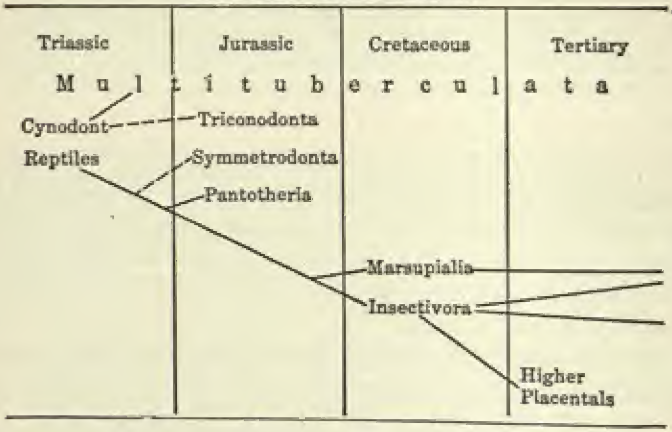


FIG. 167.—Trituberculate mammal (pantothere), *Dicrocynodon victor*, Jurassic, Wyoming. *a*, canine tooth; *b*, condyle; *c*, coronoid; *d*, angle. Twice natural size. (After Marsh.) See also Plate XVI.

been considered by good authority as the actual forerunners of that group. The molars have four or more cusps, but instead of being arranged in lineal series, as in the triconodonts, the three principal cusps are in the form of a triangle or trigon, the main one being on the inner side of the teeth in the lower jaw and on the outer side in the upper jaw. In habits the pantotheres were probably insectivorous and they have been classed with the placental mammals as primitive Insectivora. Their time range is throughout the Jurassic, and although they then became extinct as an order they may still survive in their descendants—possibly the true insectivores among other orders (see Fig. 167, also Pl. XVI).

Amphitherium, one of the oldest genera, is from the Lower Jurassic (Stonesfield slate) of England, *Amblotherium* is from the English Purbeck (Upper Jurassic), while the more familiar American forms are *Dryolestes* and *Dicrocynodon* from the Jurassic of Como, Wyoming.

SCHEME OF RELATIONSHIPS OF THE MESOZOIC MAMMALS. AFTER SIMPSON



Check on Mesozoic Mammalian Life.—Perhaps the most remarkable thing about the Mesozoic mammals is their apparent conservatism as regards evolution, for we find so little recorded change, compared with that of the reptiles during their long-drawn-out career, that we look instinctively for some inhibiting cause. After the establishment of the mammals in late Triassic time, there are no great geologic or climatic changes of a revolutionary character to quicken their evolution until the close of the Cretaceous and, while reptilian dynasties wax and wane, the trend of their evolution seems pretty well established after the early Jurassic, the remarkable types which appear later being largely the florescence which characterizes racial old age. But with the close of the Age of Reptiles came a most momentous change in mammalian evolution, when the sluggish stream of their existence was quickened into life and their remarkable radiation began. This may have been due in part to the expansion of the upland flora which, as Matthew believes, was either restricted in its development or of a sort not suitable to mammalian dietary during the Mesozoic. But it seems reasonable to suppose that the inhibition of mammalian evolution was due not so much to lack of a suitable physical and floral environment as to an overwhelming check against which these small creatures could not contend.

There is in the Yale Museum a remarkable series of mammal jaws and teeth from what is known as "Quarry 9" at Como Bluff,

Wyoming, which lies in strata of Jurassic age. Associated with them, among other reptilian remains, was a single tooth of a carnivorous dinosaur, perhaps *Allosaurus*, a tooth keen-pointed and terrible, like a curved dagger with serrated margins, and many, many times the bulk, not only of the teeth but of the entire jaws of the associated "higher" forms. This tooth, suspended like the sword of Damocles (Pl. XVI) over the head of these actually associated mammals, brings before the mind's eye broad vistas of low-lying, well-watered woodland with ever alert furry forms taking such refuge as the trees or shrubbery or occasional hiding holes could offer, in the midst of stalking terrors such as the world never saw before. That the mammals managed to maintain themselves is not surprising, for there is a teeming horde of small mammalian folk in the tiger-haunted jungles of India to-day; and that they did not dispute with the dinosaurs the realms of greater opportunity is but a logical assumption.

The Release.—If our premise be true, the great Tertiary expansion of mammals therefore is only in part the direct outcome of changing geologic conditions, the primal incentive being the removal of the reptilian check.

Archaic Mammals

This is the name given to the creatures which, in early Tertiary time, supplanted the great reptiles in their vacated habitats. They constitute the first great mammalian adaptive radiation, but one of short duration, for they were soon to be displaced in their turn by mammals of a higher sort, the so-called modernized mammals. For a while these archaic types served very well, and doubtless had it not been for a competition which they could not meet, they might have survived for a longer period; but there was written over against them the memorable indictment—"Thou art weighed in the balances and found wanting."

Defects.—There are two prime essentials to every creature's adaptation to its environment—it must have safety and food. Hence two principal structures are of paramount importance: locomotor organs, that it may flee from its enemy or overtake its prey, and efficient teeth that it may utilize such food as is available. In other words, the two organs whose contact with the environment is most intimate are the feet and teeth, and these are seen to suffer the most profound changes with the passage of time

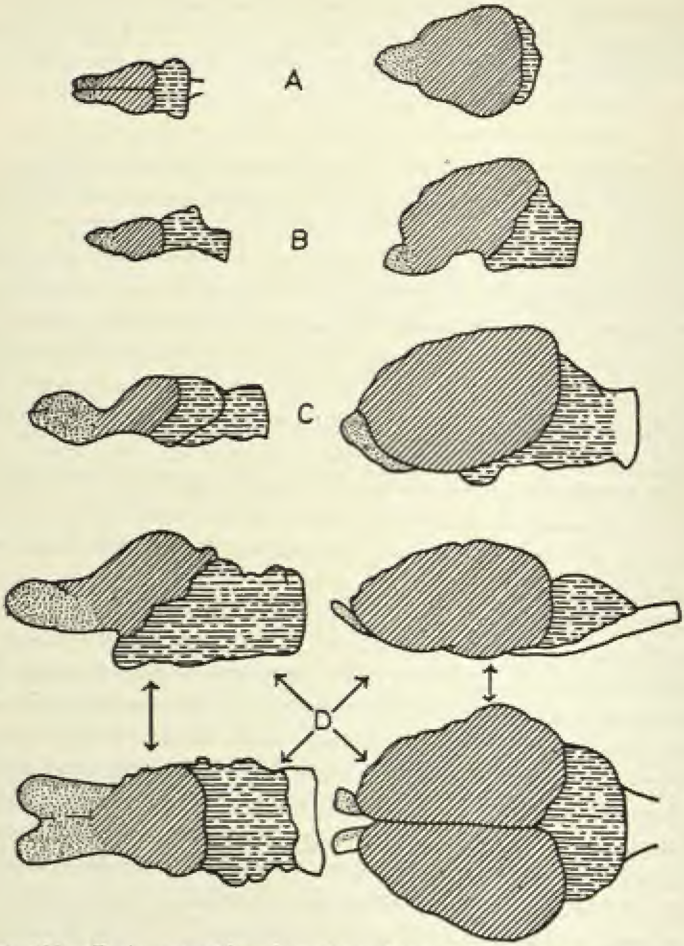


FIG. 168.—Brain proportions in archaic (left) and modern (right) mammals of similar size. Olfactory lobes (dots), cerebral hemispheres (oblique lines), cerebellum and medulla (dashes). (After Osborn.)

Arctocyon	A	*Canis*
Phenacodus	B	*Sus* (domestic)
Coryphodon	C	*Rhinoceros*
Uintatherium	D	*Hippopotamus*

and the consequent changing of the environment. Not only must these organs be adapted to immediate need, but adaptable to the inevitable changes of conditions which time will bring. Thus it is that by a study of feet and teeth so much of an animal's life conditions and consequent habits can be deduced. Add to this a structure of which the dinosaurs made but little, but which in mammalian evolution became increasingly important—the brain—and the tale of the requisites for future evolutionary success is complete.

It was specifically in these three things that the archaic mammals were deficient, for while size, strength, physical prowess, arms and armament were theirs in full measure, their feet and grinding teeth were conservative, inelastic, and incapable of meeting new conditions as they arose. Their brain too was singularly old-fashioned, generally small, but always relatively undeveloped in comparison with that of modernized mammals of equivalent bulk, especially in the part wherein the intelligence lay (see Fig. 168). Hence it is not surprising that the career of these forms was brief and that with rare exceptions they have suffered racial death and vanished as utterly as did the dinosaurs before them.

Classification.—"Nature," as Osborn says, "deals in transitions rather than in sharp lines. We can not circumscribe the archaic mammals sharply, nor be sure as yet that some of them did not give direct descent to certain of the modernized mammals. Yet the mammals of the basal Eocene [Paleocene] of both Europe and North America are altogether of very ancient type; they exhibit many primitive characters, such as extremely small brains, simple, triangular teeth, five digits on the hands and feet, prevailing plantigradism. They are to be collectively regarded as the first grand attempts of nature to establish insectivorous, carnivorous, and herbivorous groups, or unguiculates [clawed forms] and ungulates [hoofed forms]. The ancestors or centers of these adaptive radiations date far back in the Age of Reptiles. At the beginning of the Eocene we find the lines all separated from each other but not as yet very highly specialized. The specialization and divergence of these archaic mammals continue through the Eocene period and reach a climax near the top, although many branches of this archaic stock become extinct in the Lower Eocene. The orders which may be provisionally placed in this archaic group are the following:

"Marsupialia
Placentalia
Insectivora.
Tæniodonta. Edentates with enamel [-banded] teeth
Creodonta. Archaic families of carnivores
Condylarthra. Primitive light-limbed cursorial ungulates
Amblypoda. Archaic, typically heavy-limbed, slow-moving ungulates.

"This group is full of analogies, but is without ancestral affinities to the higher placentals and marsupials. There are forms imitating in one or more features the modern Tasmanian 'wolf' (*Thylacynus*), the bears, cats, hyænas, civets, and rodents of to-day, but no true members of the orders Primates, Rodentia, Carnivora, Perissodactyla, Artiodactyla have been discovered."

Of the archaic mammals we will turn our attention to three groups, of which the first is the *Creodonta* (Gr. κρέας, flesh, and ὀδούς, tooth). These forms resemble in many details the hoofed Condylarthra next to be described, but differ from them chiefly in the skull and teeth, in that they have more the aspect of a true carnivore than the condylarths which were largely of vegetarian diet. The terminal phalanges (unguals) are also more claw-like, although there are exceptions to this rule, notably in *Dromocyon* (Fig. 169, C; Pl. XVII). The skull of a creodont differs from that of a carnivore, for while it is always large for the size of the animal, there is a much smaller brain-case, thus necessitating a high crest of bone along the mid-line of the cranium (sagittal crest) to obtain sufficient surface for muscular attachment. There are widely expanded temporal or zygomatic arches for the same purpose. The teeth also differ in not being so perfectly adapted for a flesh diet as in the true carnivores. In the latter (see Fig. 43), certain cheek teeth are almost always enlarged and modified to form a wonderful shearing device, and these so-called carnassial teeth (Lat. *caro*, flesh) are, when present, *invariably* the fourth upper premolar and first lower molar, expressed thus: $\frac{p^4}{m_1}$. With the creodonts the carnassials may not be developed at all, and if they are, are variable and not necessarily, indeed rarely, $\frac{p^4}{m_1}$, and in addition they are rarely confined to a single pair of teeth but are two or more in number.

The creodonts have been divided into at least six distinct fami-

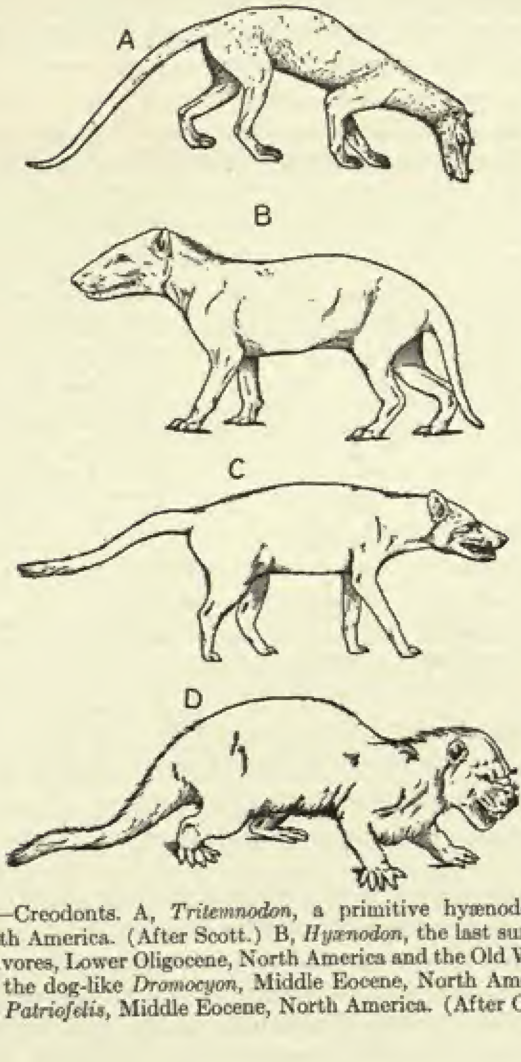


FIG. 169.—Creodonts. A, *Tritemnodon*, a primitive hyænodont, Middle Eocene, North America. (After Scott.) B, *Hyænodon*, the last survivor of the archaic carnivores, Lower Oligocene, North America and the Old World (After Osborn.) C, the dog-like *Dromocyon*, Middle Eocene, North America. (After Osborn.) D, *Patriofelis*, Middle Eocene, North America. (After Osborn.)

lies, of which but one probably gave rise to true carnivores, the rest dying out one after another until by Upper Oligocene time none were in existence. The creodonts foreshadow the true carnivores in a number of ways, in that certain of them were bear-like (*Arctocyon*), others dog-like (*Dromocyon*) or otter-like (*Oxyæna*, *Patriofelis*), some like the minks (*Sinopa*), others cat-like (*Dissacus*) or resembling hyænas (*Hyænodon*). The last genus is of especial interest because together with its Old World ally *Pterodon*

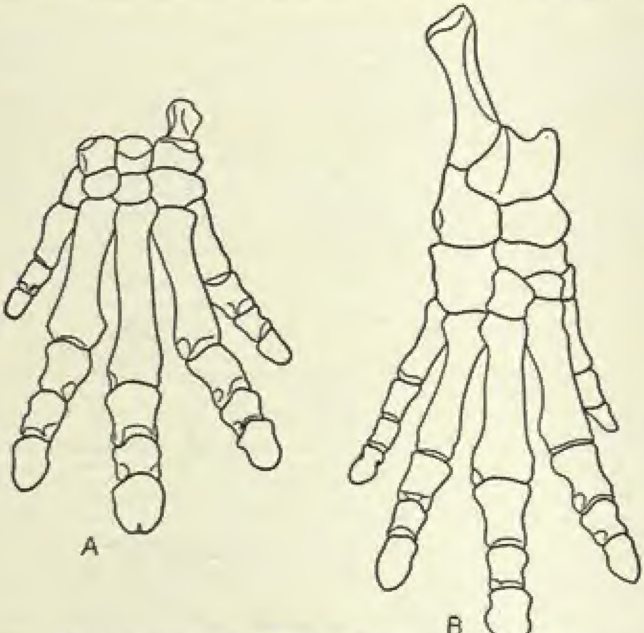


FIG. 170.—Fore (A) and hind (B) feet of *Phenacodus primævus*. (After Lull.)

it is the last creodont survivor, existing until the Middle Oligocene. One form, *Andrewsarcus*, from Mongolia, attained gigantic size, the skull alone measuring nearly a yard in length.

The *Condylarthra* (Gr. κόνδυλος, knuckle, and ἄρθρον, joint) were a group of very primitive ungulates which, aside from the implied differences in diet, paralleled the Creodonta closely, for in both groups there was the same generalized type of body with a long heavy tail and rather stocky, more or less cursorial limbs. There were, however, relatively few of the condylarths, but four families being recognized as against six for the creodonts. They

range in time from Paleocene and Lower Eocene, but very little is known as yet of their geographical extent. Scott says of them: "They may be looked upon as the connecting link between the clawed and hoofed mammals and therefore ancestral to most, or perhaps all of the ungulate orders." One of the condylarths, *Phenacodus* (Figs. 170; 171; Pl. XVIII), was hailed by its discoverer, Professor Cope, as the five-toed ancestor of the horse, but this is now known to be impossible as it is too large and too highly specialized in certain directions, although very primitive in others, and also too late in time to be the founder of the great equine lineage. This genus, from the Wasatch beds (Lower Eocene), ranged in size from a fox to a small sheep. While the canines were tusk-like, they were not large, and the grinding teeth were low-crowned and of simple pattern, suited undoubtedly to a rather succulent herbage. The skull was long and low, with a well developed sagittal crest and, while that portion of the cranium behind the orbits was relatively long as with most primitive skulls, the brain-case was of very small capacity. The feet are five-toed, semi-plantigrade, and built on a very primitive plan. *Phenacodus* and the earlier *Euprotogonia*, represent the family Phenacodontidæ while the other family, Meniscotheriidæ, embraces but a single known genus, *Meniscotherium*. These forms, while contemporaneous with the phenacodonts, were more advanced in tooth structure, for the cusps of the grinders have begun to assume a crescent shape such as one often finds in the higher odd- and even-toed ungulates. The body and tail were long and the limbs, while long, resemble so much those of the Hyracoidea of Africa (see page 557) as to cause the inclusion of *Meniscotherium* in that group by certain authorities. Others have considered the Hyracoidea to be surviving condylarths. There are, however, no very good grounds for such an assumption. The Condylarthra are of interest, however, in that they represent or were very similar to what was probably a very widespread group of primitive ungulates out of which, possibly, all of the other orders

FIG. 171.—Cursorial archaic mammal, condylarth, *Phenacodus primævus*, Lower Eocene, North America. (After Osborn.)

of ungulates arose. The genera which we know could not have been the direct ancestors, but they show us the nature of the ungulate ancestry.

The *Amblypoda* (Gr. ἀμβλύς, blunt, and πούς, foot), or short-footed ungulates, are another group of hoofed forms, among which were some that attained a huge, almost elephantine size and in spite of a basic primitiveness developed a superficial specialization of a very remarkable sort. Their geologic range is throughout the Eocene period, when they in their turn suffered extinction. Four families are recognized, of which the two most primitive are both Paleocene in distribution. *Pantolambda*, the type of the second family, while undoubtedly an ungulate, shows many points of similarity with the creodonts. It is described as having a head and body somewhat smaller than those of a sheep, and much shorter legs. The body and tail had somewhat the proportions of the larger cats, and the skull, as with the condylarths, was long and low, with small brain capacity and prominent sagittal crest. The limbs were very short and relatively heavy, with five spreading toes on each foot.

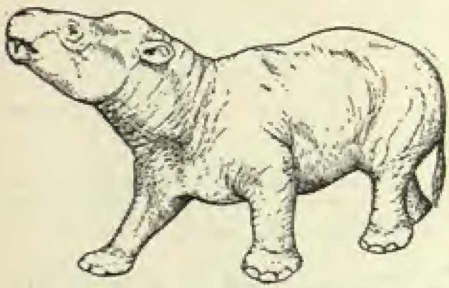


FIG. 172.—*Coryphodon*, a swamp-dwelling amblypod, Lower Eocene, North America. (After Osborn.)

Coryphodon (Fig. 172) represents the third family and is in many ways a remarkable beast. The different species vary in size from a tapir to an ox, and thus are the largest forms we have so far considered. They were heavy, unwieldy animals whose short powerful limbs and spreading feet point to swamp-dwelling if not aquatic habits. The skull was large and flattened in such a way that no median crest is visible, nor are there any indications of horns such as the next genus possessed. The canine teeth were developed into huge flaring tusks suggesting those of the swine. Altogether it was a heavy sluggish brute whose very small brain gives evidence of great stupidity.

Uintatherium (*Dinoceras*) (Fig. 173) represents the last family of amblypods and in many ways—size, up to seven feet in height, dentition, and horns—was by far the most specialized, in fact

grotesquely so. Its limbs were graviportal, quite like those of the Proboscidea (see Chapter XXXV) and like them an adaptation to carry the creature's great weight. The elephant-like characteristics extended also to the body, but there the resemblance ceased, for the skull was totally dissimilar in that it was extended upward into a series of horn-like prominences. These consisted of a pair upon the nose, which from their appearance may have borne dermal horns like those of rhinoceroses. The second pair were higher, with bluntly rounded ends, and were probably not sheathed with horn but covered with skin as in the giraffe. There was also a third pair, massive structures, 8 to 10 inches high, which again could not

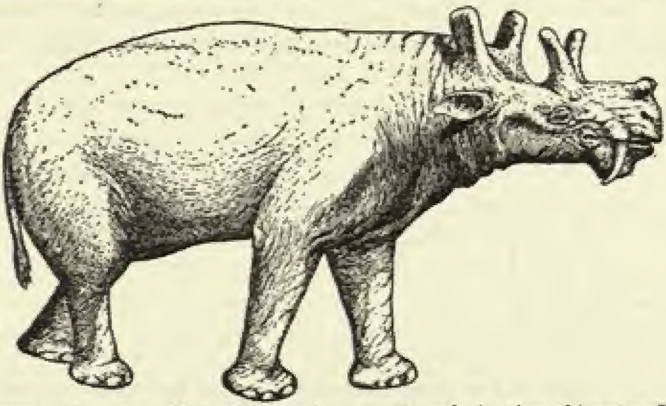


FIG. 173.—Horned amblypod, *Uintatherium*, the culmination of its race, Upper Eocene, Wyoming. (After Osborn.)

have borne horny sheaths. There was a high transverse occipital crest at the hinder end of the skull connecting the posterior pair of horns and giving, together with the prominences, a unique basin-shaped character to the top of the skull. Another remarkable feature lay in the greatly developed canine teeth, which were curved sabers in some genera and spear-shaped in others, and were doubtless important weapons. Both the tusks and horn prominences were apparently better developed in the male than in the female, for their variation constitutes about the only difference seen in certain skulls. There is no indication of a proboscis, as the nasal bones, which are long and prominent in *Uintatherium*, are invariably shortened whenever that useful organ develops. The molar teeth *Uintatherium* were very conservative, for while one may trace a very marked evolution in the skull and tusks, these impor-

tant organs hardly change at all (see Fig. 174). The brain also was absurdly small for so large a creature. The armament of *Dinoceras* may have served a useful purpose but one is constrained to believe that, together with the relatively great size, it indicates racial senility —the extreme of over-specialization attained by a primitive stock.

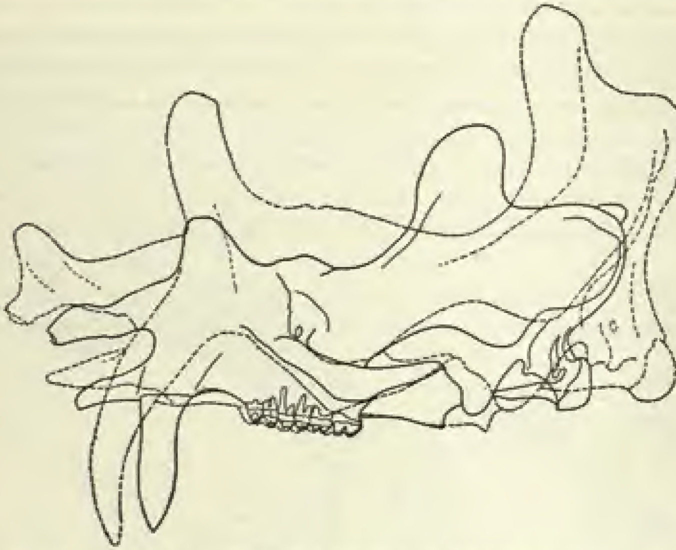


FIG. 174.—Skulls of Uintatheres, showing that while the rest of the skull has increased markedly in size, the length of the tooth row remains approximately the same. Solid line, *Uintatherium mirabile;* broken line, *Tinoceras ingens.* (Adapted from Marsh.)

Fate of the Archaic Mammals.—The archaic mammals as such have long since vanished from the earth, and were it not for their remains entombed in the Eocene rocks we would be unaware that they ever existed. Theirs was a brief span compared with that of the reptilian hordes and also with that of their mammalian successors; but for a while they throve mightily until competition with creatures of a better sort became too great for them to bear. That they strove to meet this competition is evident, for certain of the later creodonts, notably *Patriofelis* and the powerful *Harpagolestes* and especially *Andrewsarcus* of Mongolia, increased materially in bodily size, while the hyænodonts actually increased the bulk of the brain, which aided in making them the sole survivors of the group after the close of the Eocene. Competition was doubt-

less, therefore, a prime cause which led to the extinction of these forms. We have argued racial old age in *Uintatherium*, but if that be deemed insufficient in itself, we have the noteworthy fact that where evolution of an animal runs to the development of tusks and horns, possibly favored by sexual selection, the grinding teeth are apparently neglected and are apt to show arrested development. And bulk is fatal where correlated with inadequate feeding mechanism, and with brain power not adequate to enable the females to defend and care for the young as well as to meet new conditions of life.

Thus the fate of the archaic mammals was, first, extinction, and, secondly, transmutation of a few—a very few—into higher types. There remains yet a third possibility, and that is emigration, not of the later but of the earlier sorts, across the southern land-bridge into South America, where together with a certain admixture of other stock they may have given origin to part of the remarkable South American fauna which rose and flourished during the long period of Neogæan isolation. Others, passing beyond the limits of South America, may have crossed an Antarctic land-bridge into Australia, where as marsupials they still persist. If, on the contrary, the entire marsupial order is to be considered archaic, the conclusion that they may still be surviving in these remote forms and in the American opossums is tenable. There is a further possibility that the American Edentata, sloths, armadillos, and their allies, should be included in the group. They also have survived because they found asylum in isolated South America.

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CHAPTER XXXIII

INCURSION OF MODERNIZED MAMMALS AND EVOLUTION OF CARNIVORES

We have spoken of the modernized mammals in contradistinction to the archaic forms. It is necessary now to define the former more precisely. They include practically all existing mammals and some which have become extinct together with their forebears, such as:

Carnivora or fissiped and pinniped (seals) carnivores.

Rodentia, gnawing animals.

Perissodactyla, odd-toed ungulates.

Artiodactyla, even-toed ungulates.

Proboscidea, elephants and mastodons.

Primates, lemuroids and monkeys.

Insectivora, insectivores, included by some authorities among the archaic mammals.

Cetacea and Sirenia, whales and sea-cows.

In contrast with the archaic forms, the modernized types are all creatures of high potentiality, and, where they became extinct, were rather the victims of circumstance than creatures which died because of lack of adaptability, although certain groups seem to have run a natural course and their extinction was heralded by evidences of apparent racial senility.

As the archaic forms were characterized by lack of progressive brain and feet and teeth, so the modernized races were distinguished by the possession sometimes of one (primates), sometimes of two (elephants), again by all three (horses) of these destiny-controlling organs, but in general the modernized animals were progressives, highly adaptable forms.

Place of Origin of the Modernized Mammals.—The simultaneous appearance of the earliest of the modernized mammals in Europe (lat. 50° N.) and North America (lat. 40° N.) points to some contiguous land-mass as the original home of these creatures. Hence there has been assumed the existence of a grand northern common center of evolution and dispersal, both for plants and

animals. A glance at the map, Fig. 7, drawn on the north polar projection, will show how logical such an assumption is, and, with the evidence very clearly before us of the repeated recurrence of a land-bridge across what is now Bering Strait, how readily migrants from a circumpolar land could follow the three great continental radii to the south, arriving synchronously in widely separated lands. Of course the theory of circumpolar origin of these mammals assumes a climate far different from that which now characterizes this region; but that it was formerly warm and equable is abundantly proved by the finding on the coast of Greenland of the remains of a sub-tropical flora. Thus Heer describes cycads and associated species of plants in the Lower Cretaceous as indicating a mean temperature of 70° to 72° F.— a temperature equal to that of Cuba—and the same flora existing in Spitzbergen and in Alaska proves that this temperature was widely distributed.

Deployment.—There is always a tendency on the part of every group of animals, as their numbers increase, to spread from their ancient home along lines of least resistance, provided no climatic or other insuperable barriers are to be overcome, and that may well have been one very potent cause for the southward migration of the modernized hordes. But there was an additional incentive, for throughout the early Tertiary there is evidence of climatic variation and of a very gradual cooling of the northern regions and a consequent southward retreat of the higher plants and mammals which occurred as a succession of migratory waves. In this way there came, first, the least hardy like the insectivores and primates, the latter especially depending so largely upon the tropical forests for their sustenance that any change either in extent or character of their habitat would be reflected in their distribution at once. Perissodactyls and artiodactyls also came speedily, and the true carnivores—primitive dog-like forms—likewise soon appeared. There is reason to believe, however, that throughout the whole pre-Pleistocene Cenozoic period the northerly region (Holarctica) was highly favorable to the evolution and migration of the higher forms of the Mammalia. It must be remembered, however, that the actual center from which these animals suddenly spread into Europe and North America is still hypothetical and will not be determined until the Paleocene fossil mammal beds in the unexplored portions of America and Asia shall have been discovered.

Whatever the exact place of origin, the result of the incursion of the progressive forms was their speedy usurpation of the habitat of the unprogressives and, as we have seen, the gradual elimination of the latter, largely through an unbearable competition. We shall now speak of these modernized mammals, turning our attention to the following well known and highly interesting groups, some of which, notably the horses, played no little part in the widespread acceptance of the evolutionary hypothesis. These groups are:

1. Carnivora, especially the felines.
2. Whales.
3. Proboscidea, mastodons and elephants.
4. Horses.
5. Camels.
6. South American mammals.
7. Primates, with especial reference to mankind.

Carnivora

The division of the flesh-eating mammals into creodonts and true carnivores has been discussed and the main distinctions emphasized (page 508). The modernized forms are also divisible into two groups, the Fissipedia (Lat. *fissus*, cloven, and *pes*, foot) or land carnivores, and the Pinnipedia (Lat. *pinna*, feather, fin) or seals and sea-lions. The latter do not possess the carnassial teeth and their derivation from any known fissiped stock is doubtful. They may well represent an independent line of descent from the creodonts. The same may be true of the whales.

The fissiped carnivores show the following diagnostic characters:

1. Good brain, moderately large and well convoluted.

2. Carnassial teeth = $\frac{p^4}{m_1}$, premolars in front more or less sharp-pointed and compressed; molars behind tuberculated for crushing.

3. Clavicle (collar-bone) vestigial or absent.

4. Limbs mobile, with the radius and ulna of the fore arm and the tibia and fibula of the lower leg complete and separate.

5. Digits clawed, never fewer than four.

The principal families are:

Canidæ.—These embrace the foxes, dogs, and wolves, the most primitive of existing carnivores, cosmopolitan in their distribution, even having attained Australia, though doubtless by the agency of man. They appear first in the Upper Eocene of Europe, are abundant in the Miocene fauna of Europe and North America, and reach India and South America

by early Pliocene time. At present at least 104 species of canids are extant and more than 160 fossil species have been described.

Ursidæ.—The bears are omnivorous rather than strictly carnivorous and lack the carnassial teeth. Their feet also are plantigrade compared with the digitigrade character of those of most of the order. Bears are widespread to-day, principally in the northern portions of both hemispheres. In the Old World they extend southward to the Atlas Mountains in northern Africa and to southern India, Borneo, Sumatra and Ceylon. They are also found in the Andean highlands as far south as Bolivia and Chile. They are, however, entirely absent from the Ethiopian and Australian realms. The origin and evolutionary history of the bears is undiscovered, as the earliest recorded fossils are in the Miocene of the Old World; by Upper Pliocene they had reached eastern Europe but up to 1916 they were unknown in the New World in rocks older than the Pleistocene. A Pliocene bear, however, has recently been reported from Oregon (Merriam).

FIG. 175.—Various carnivora. A, hyæna, *Hyæna striata;* B, bear, *Ursus arctos;* C, dog, *Canis familiaris;* D, marten, *Mustela martes;* E, cat, *Felis domestica;* F, genet, *Genetta tigrina.* (After Haacke.)

Procyonidæ.—The procyonids, the raccoons and their kin, with one Asiatic exception are entirely confined to the New World, especially

tropical America. Geologically they range upward from the primitive Miocene genus *Phlaocyon*, which is the annectant form between this family and the Canidæ, although the grinding teeth and plantigrade feet of the raccoon have caused its inclusion by certain authorities with the bears.

Mustellidæ.—This family, which contains the weasels, polecats, badgers, and otters, while especially abundant in North America is found the world over, except Australia. Its members are, however, rare in Africa and South America. They are known from the Upper Eocene in Europe and from the Oligocene of North America, and one Miocene form, *Megalictis*, was gigantic, the skull alone equalling that of a black bear.

These four families are known collectively as Arctoidea or bear-like forms, while the three remaining ones, Viverridæ, Hyænidæ, and Felidæ, are called Æluroidea (cat-like). With the exception of the cats this latter group is entirely confined to the eastern hemisphere, which was probably also their original home.

Viverridæ.—These are the civets, genets, and mongooses, and are limited largely to the Ethiopian and Oriental realms, only a half-dozen species being found outside of these areas. The curious Madagascar genus *Cryptoprocta*, the fossa, forms a connecting link between this family and the cats. About thirty species are known fossil, chiefly from the European Tertiary, the genus *Viverra* itself having persisted since latter Eocene time.

Hyænidæ.—The hyænas are creatures of very dubious repute, as they are largely eaters of carrion. In spite of a rather dog-like appearance, their affinities lie with the Viverridæ, from which they lately arose. They are confined to-day to tropical Asia and Africa, but formerly had a much wider range.

Felidæ

The cats are in many ways the most highly specialized of carnivores, chiefly in their dentition, for the carnassial here reaches the height of perfection as a shearing tooth; the molars, on the contrary, are almost entirely lacking. Another specialization lies in the retractile claws, characteristic of all Felidæ except the cursorial hunting leopard or cheetah (*Acinonyx*), which is the swiftest mammal and shows a number of dog-like convergences in limbs and feet. The working of the retractile claws is as follows. The ungual or claw-bearing phalanx is capable of a wide vertical range of movement and has attached to its upper side an elastic ligament which would keep the claw permanently raised were it not for an antagonistic muscle and tendon attached to the lower side. The contraction of this muscle pulls the ungual downward, thus protruding the claw and at the same time stretching the elastic ligament. Relax the muscle and the elasticity of the ligament again withdraws the claw. This permits the cat to move silently in stalking its

prey and at the same time provides prehensile organs of high perfection for securing it.

Distribution.—Cats are to-day world-wide in their distribution with the exception of Madagascar and Australia, the Old World producing the most notable living species, such as the lion (*Felis leo*), the tiger (*F. tigris*), the leopard (*F. pardus*), the ounce or snow leopard (*F. uncia*), and others including the supposed ancestor of our domestic cat, the caffre or Egyptian cat (*F. caffra*). In the New World the most noteworthy are the puma (*F. concolor*), the jaguar (*F. onca*), and the lynxes and caracals.

Fossil Cats.—But it is the fossil felines which are in many ways of the greatest interest, for they include not only the ancestors of the modern forms, but the now extinct saber-tooths—creatures whose endowment of effective weapons puts them in the very forefront of the carnivorous hordes as efficient beasts of prey. Thus the Felidæ are divisible into two phyla or subfamilies, the Felinæ or biting cats, the race to which all existing felines belong, and the Machairodontinæ or saber-tooths, the stabbing cats whose line has ceased to exist. They show many points of contrast in body, limbs, and tail, but especially in skulls, jaws, and dentition, and, as we shall see, these distinctions arose in the course of evolution from a single as yet unknown stem through adaptation to contrasting types of prey, for the saber-tooths were relatively slow of foot, and their rise, culmination, and decline is so intimately associated with that of the slow-moving, thick-skinned ungulates, elephants, rhinos, swine, and especially the ground sloths, that the conclusion that we have here the proper association of predatory animals and their usual victims is irresistible. On the other hand, the swift-footed biting cats are in like manner associated with the thin-skinned cursorial ungulates—as they are to-day—and the inference is that they in their turn were adapted to such a source of food.

The contrasting anatomical features are: Felines—limbs less robust, more cursorial, toes tending to reduce; Machærodonts—limbs shortening, more robust, digits never fewer than five. In the Felinæ the tail was long, in the saber-tooths it became progressively shortened, especially in the final form, *Smilodon*.

Dentition.—In the felines or biting cats the carnassial is relatively smaller and the premolars in front of it are less reduced than in the saber-tooths. But it is in the development of the canine

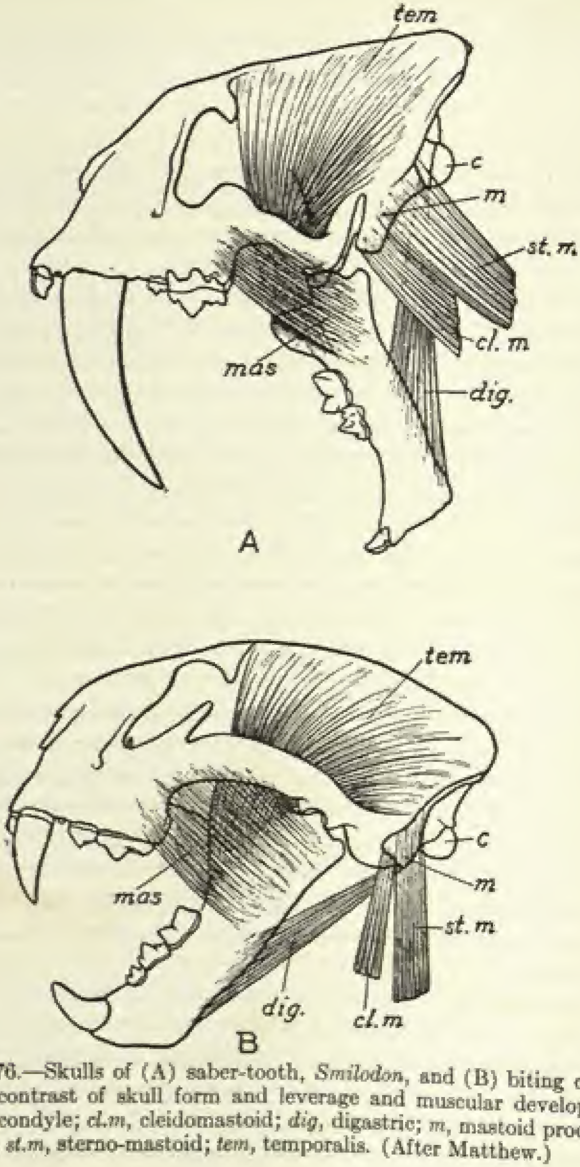

FIG. 176.—Skulls of (A) saber-tooth, *Smilodon*, and (B) biting cat, *Felis*, showing contrast of skull form and leverage and muscular development. *c*, occipital condyle; *cl.m*, cleidomastoid; *dig*, digastric; *m*, mastoid process; *mas*, masseter; *st.m*, sterno-mastoid; *tem*, temporalis. (After Matthew.)

that the most marked distinction is seen, for while in the Felinæ the upper and lower tusks are more nearly equivalent in size and power, in the machærodonts the lower ones are reduced to a size not much greater than that of the incisors. The upper canines, on the contrary, have become thin curved daggers of relatively enormous length, showing the same fine serrations on their cutting edges that we saw in the teeth of the carnivorous dinosaurs! It is these great saber-like tusks which give the popular name to the group.

Skull.—There is a marked difference in the form of the skull in the two phyla, especially when seen in profile, and the principal purpose of this modification in the saber-tooths is to obtain greater leverage and so render more effective the downward stabbing stroke of the tusks. A glance at the diagram of the skulls of *Felis tigris* and *Smilodon*, drawn to the same scale (Fig. 176), will render this clear. The principal distinction lies in the rear of the skull or occiput and in the arch of the face. In *Felis* the cranial arch is highest just behind the orbits and diminishes both toward the front and toward the rear, so that the occiput is comparatively low. In *Smilodon*, on the other hand, the rear of the skull is highest and the face slopes downward and forward, the sabers continuing the line of the curve. The condyle for the articulation with the neck is on a level with the tooth line in *Felis* and the mastoid processes behind the ear openings are inconspicuous; in *Smilodon*, on the other hand, the condyles are high and the mastoid processes extend far below them. These processes are for the insertion of the sternomastoid and cleidomastoid muscles whose combined function it is to depress the skull. Their value in the saber-tooth is at once apparent, as they are the muscles which produce the downward stroke of the head by which, with terrible efficiency, the tusks are driven into the victim. A well-rounded condyle in *Smilodon* points to great freedom of movement in the vertical plane. The muscles of the dorsal side of the neck, which raise the head, were alike powerful in both forms.

Jaw.—There is a marked distinction in the lower jaws of the saber-tooths as compared with the biting cats, more marked in some respects in the earlier types such as *Hoplophoneus* than in *Smilodon*. For here the jaw is lighter and has less powerful muscles, as the diminished coronoid process and other muscle-insertions show. The jaw was capable of being opened more widely in the saber-tooth, although the yawn of a modern tiger is a memorable

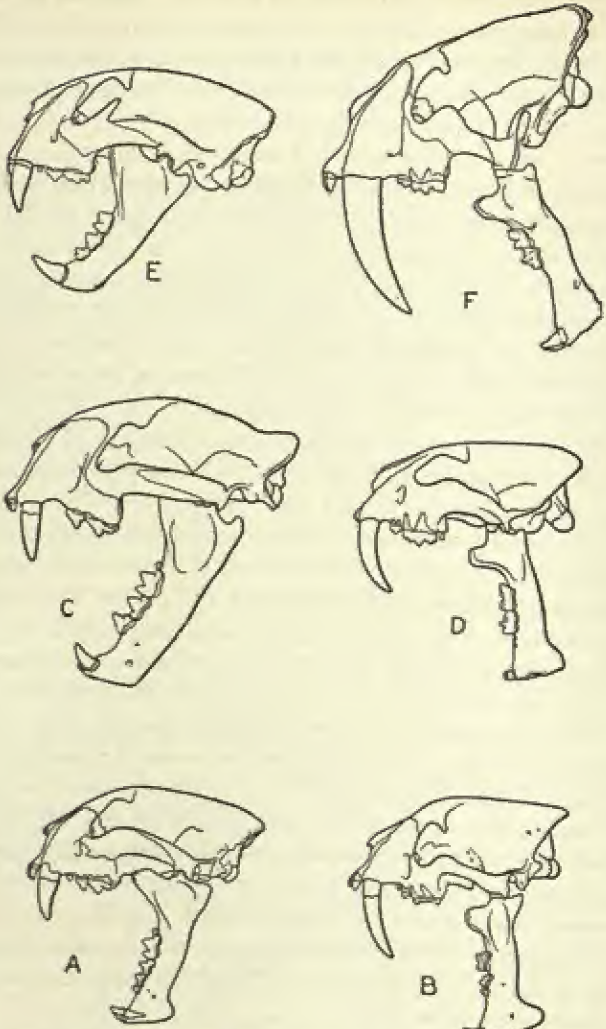

Fig. 177.—Skulls of felines (biting cats, A, C, E) and machairodonts (saber-tooths, B, D, F). A, *Dinictis*, and B, *Hoplophoneus*, Oligocene; C, *Nimravus*, and D, *Machairodus*, Miocene; E, *Felis*, and F, *Smilodon*, Pleistocene. (After Matthew.)

sight. In the earlier saber-tooths the front portion of the lower jaw is continued downward into a distinct flange for the protection of the tusk, a feature which the totally unrelated amblypod *Uintatherium* (Fig. 173) also shows. In later forms, with the enormous extent of the tusks such a protection becomes impracticable and the flange almost entirely disappears. The chin of the saber-tooths, however, never shows the rounded character of that of the biting cats.

PHYLETIC TABLE OF FELIDÆ

(Modified from Matthew)

	FELINÆ, BITING CATS	MACHAIRODONTINÆ, SABER-TOOTHS
Recent	*Felis* (Lat. cat)	Extinct
Pleistocene	*Felis*	*Smilodon* (carving-knife tooth)
Pliocene	*Felis*	*Machairodus* (dagger tooth)
Miocene	*Pseudælurus* (false cat)* *Nimravus* (hunter ancestry)	*Machairodus*
Upper Oligocene	*Nimravus* *Dinictis* (terrible weasel)	*Hoplophoneus* (armed slayer)
Lower Oligocene	*Dinictis* *Ælurictis* (cat weasel)	*Hoplophoneus* *Eusmilus* (well equipped as to the jaw)
Eocene	Undiscovered Miacidæ, probably Asiatic	

* *Pseudælurus* may represent a new immigrant unrelated to *Nimravus* (see text, page 527).

Ancestry.—The cats seem to have had their initial evolution in the great Asiatic adaptive radiation center, whence they spread the world over. It is only in North America, however, that the paleontological series is sufficiently complete to reconstruct a phylogeny such as the above. The Asiatic Eocene ancestry is as yet unknown.

Feline Phylum.—*Dinictis* (Figs. 177; 178) is the most primitive of cats, but is, nevertheless, despite the fact that Matthew places it in the biting cat phylum, a saber-tooth, as the elongated upper and reduced lower canines, the flattened chin, and the protective jaw-flange show. Scott looks upon this form as the somewhat modified survivor of the ancestral stage, and representing very nearly the common starting point of both the feline and machærodont

subfamilies. As compared with its contemporary, *Hoplophoneus* (Fig. 179), the limbs in *Dinictis* are longer and more slender, implying greater cursorial powers. The limbs also retain more primitive features, and the smaller feet, with their less developed claws, did not have the clutching power of those of *Hoplophoneus*. Altogether *Dinictis*, while showing certain saber-tooth characteristics, was speedier and less capable of holding a struggling prey until the stabbing tusks could manifest their effectiveness. It was therefore tending toward the adaptations of the modern cats, which is reason for considering it the first recorded member of their line rather

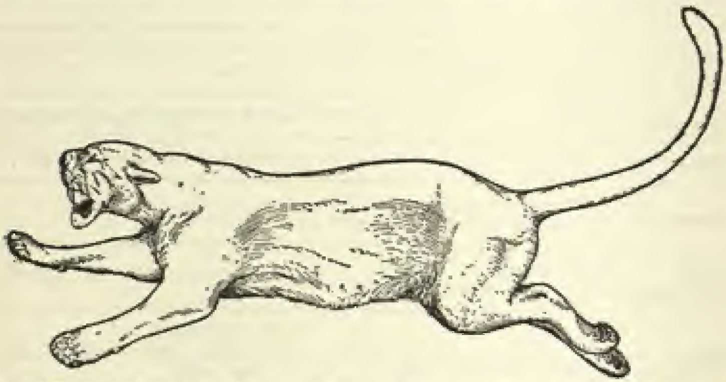

FIG. 178.—Restoration of an ancestral feline, *Dinictis*. (After Knight, from Osborn.)

than the common ancestor of both phyla. *Dinictis* is confined to the American Oligocene.

The genus *Nimravus* (Fig. 177,C) is still more like the modern cats in the general aspect of the skull and dentition. The canines are more nearly of a size, although the upper ones are still decidedly the larger. The mastoid process is not at all prominent, the lower jaw lacks the flange, and the chin is becoming rounded. The limbs are long and slender as in *Dinictis*, but the foot, instead of being five-toed, has but four, of which the lateral ones are shortened; while all of them bore only partially retractile claws. In general, the limbs are dog-like, resembling those of the living cheeta (*Cynælurus*) of which we have spoken and which may be a lineal descendant of these so-called "false saber-tooths." *Nimravus* is found in the Upper Oligocene and Lower Miocene of North America and the Miocene of France.

In *Pseudælurus* the canines are normal and the jaw has neither flange nor an angulated chin. The skeletal characters and much of the skull are as yet unknown. This cat is found in the mid-Miocene of France and again in the Middle and Upper Miocene of Nebraska and Colorado. It is an undoubted ancestor of *Felis*, though it may not have been derived from *Dinictis* at all, but is rather, as Scott believes, a new migrant both into Europe and North America from the Asiatic home of the race. That there were two phyla Scott does not deny; he does object, however, to Matthew's attempted derivation of biting cats from primitive saber-tooths such as *Dinictis*, claiming that "this view runs contrary to the supposed 'law of the irreversibility of evolution,' a rule which many authorities look upon as well established."

The law of the irreversibility of evolution applies rather to the impossibility of *regaining* a lost anatomical structure, not, as Scott would imply, to the reduction of a highly specialized one; and while the parallelism is not exact, the proboscideans to be discussed in a later chapter underwent somewhat the same evolution as that which Matthew postulates for the cats, in that a highly modified and elongate jaw symphysis subsequently shortened and simplified and the upper tusks, large structures in all known prehistoric elephants, are to-day becoming vestigial in the existing Indian species, even in the males.

Felis (Figs. 176,B; 177,E) is the final genus of the biting cat phylum and needs no further description than that given above. Geologically it dates back to the Pliocene and was represented in the North American Pleistocene by a large species, *Felis atrox*, of a size greater than a lion and ranging over the southern half of the continent. Huge specimens of *F. bebbi*, a somewhat different species, have been found in the Rancho La Brea asphalt of southern California in association with the great saber-tooth *Smilodon californicus*. But although the skulls of the latter are numbered by the hundreds, as many as thirty having been found within the space of three or four cubic yards, those of the former are very rare, as though their habitat and habits differed materially, and the lion-like form, not being adapted to prey upon the great brutes which were caught in the tar, did not often venture within the limits of its fatal grasp.

Saber-Tooth Phylum.—Turning to the saber-tooth phylum, there is little doubt that the Oligocene *Hoplophoneus* (Figs. 177,B;

179; Pl. XIX) was the direct ancestor of the saber-tooth line. In this genus the upper canine was long, thin, curved, and finely serrated along both edges, but the lower canines were hardly larger than the incisors. The skull was longer than in modern cats and in every way resembled a smaller and more primitive edition of that of *Smilodon*. The lower jaw was relatively much stouter than in the latter and the flange was so deep that the tusks were completely protected and could only be used when the mouth was open. *Smilodon*, on the other hand, could have used the tusks very effectively with the mouth closed; whether it did or not is a matter of opinion which cannot now be decided. The body and tail of *Hoplophoneus* had more the proportions of a modern leopard, but the limbs were more powerful, although far less so than in *Smilodon*. The character of the fore limb-bones implies great freedom of rotation of the fore paw, showing it to have had a more general use than in modern

FIG. 179.—Restoration of an ancestral saber-tooth, *Hoplophoneus*. (Modified after Knight, from Osborn.)

cats. The feet were small, five-toed, but with fully retractile claws. Thus Merriam says: "The presence of long, knife-like canines is correlated with powerful grasping feet possessing highly developed retractile claws. With its powerful feet the animal clung to its prey while it struck repeatedly with its thin, sharp sabers."

Machairodus (Fig. 177,D) is the Miocene to Pleistocene representative of the saber-tooth phylum, known from very fragmentary material in North America, but from practically perfect skulls in the Miocene of France. The skull is like that of *Smilodon*, but somewhat more primitive, being longer, with a smaller braincase and muscular crests. The mastoid processes for the insertion of the stabbing muscles of the neck were less developed. The jaw, on the contrary, was proportionately heavier than in *Smilodon* and the protective flange much larger. It was insufficient, however, fully to protect the canine when the mouth was closed. *Machairodus* is in many respects midway between *Hoplophoneus* and *Smilodon*, but whether or not any of the American Miocene and Pliocene

forms are surely of that genus cannot be decided until skulls are found. The jaws which are known, however, are quite similar.

The genus *Smilodon* (Figs. 176,A; 177,F; 180; Pl. XX) terminates the series of saber-tooth cats and has already been characterized in contrast with *Felis* (page 521). It seems to be exclusively New World, the European Pleistocene saber-tooths belonging to the more conservative Machairodus. *Smilodon* was originally discovered in South America (Pampas formation), but its presence in North America is abundantly proved by the profusion of its remains at Rancho La Brea. As it is often found in association with ground-sloths (*Mylodon*, etc.) which are unknown in the Old World, its final specialization over the more conservative *Machairodus*,

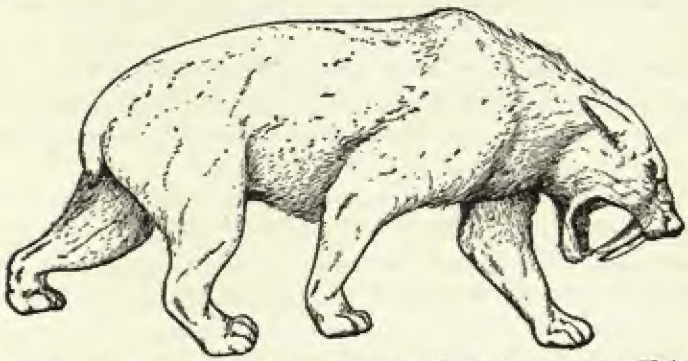

Fig. 180.—Restoration of the final saber-tooth, *Smilodon*. (After Knight, from Osborn.)

its European contemporary, may well have been a special adaptation to destroy and devour the great sloths in particular, rather than the other pachyderms which formed the dietary staple of saber-tooths in general.

There is preserved in the Museum at Buenos Aires a skull of *Smilodon neogæus*, casts of which may be seen in many museums, in which one of the tusks is locked fast by its tip between the equivalent canine and incisor of the lower jaw. This has been cited as argument for the belief that these structures had grown so huge as to become an actual menace to the individual, causing in the present instance a case of mechanical lockjaw which was followed by death from starvation. The analogy, although not precise, lies with the deer whose antlers are occasionally locked in combat resulting in the speedy death of the contestants, either

from starvation or because their subsequent helplessness renders them an easy prey to human or other enemies. This has been taken as an argument in favor of momentum in variation (Loomis), by which is meant orthogenetic variation, possibly guided in part by natural selection, but which, instead of ceasing when the point of greatest usefulness is attained, breaks away from selection control and continues to increase even to the limit of disaster.

Merriam speaks of the destructive apparatus of the saber-tooth tiger as "one of the most deadly combinations that has been found in any flesh-eating animal, but like the delicate mechanism of the high-power gun there seem also to have been great possibilities for becoming disabled; and if the long, thin sabers were once broken the saber-tooth would be less effective than the other large cats. . . . In a large number of specimens found there is evidence of fracture or loss of one [see Plate XX] or both sabers long before the death of the animal, so that the extreme specialization of this creature may have led to a stage at which accidents occurred so commonly as to destroy the type."

Matthew, on the contrary, cannot believe "that such a noxious character could be developed to the point of seriously reducing the expectation of life of the individuals in which it was present, much less of being the direct cause of the extinction of a race." He believes that in *Smilodon*, the immense development of the canines "made them highly efficient weapons for a particular mode of attack and was an essential element of its success in its especial mode of life, not a hindrance or bar to its survival."

As we have seen, the evolution of the biting cats, swift of foot and powerful of jaw, was correlated with that of the thin-skinned cursorial ungulates, their normal prey. With them, these cats spread and waxed strong and powerful, and with their diminution in the New World the felines diminished. In the Old World, on the contrary, both great cats and great game of the cursorial sort are still numerous.

The machairodonts, on the other hand, increased *pari passu* with the heavy, slow-moving, thick-skinned forms and with them they diminished, for both these ungulates and ground sloths and their saber-tooth enemies are extinct in the New World, while in the Old the great ungulates are rare and so far between that the sabertooths have entirely disappeared there as well. Since their day the elephants and rhinos, once their stature is attained, fear no foe but

man, although the lions and tigers do assail their young and thus they are held in check. It is the old story of high and narrow specialization and the dependence upon a peculiar sort of conditions and of food—eliminate those conditions or the food and the very specialization which was once a mark of adaptability now makes the race inadaptable and its doom is sealed.

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CHAPTER XXXIV

CETACEANS

Place in Nature.—To the Cetacea belong the whales and porpoises, a remarkably clearly defined group, and yet one showing convergences toward several other unrelated orders of animals. They are lung-breathers and hence secondarily aquatic forms, a characteristic which, together with their warm blood and their viviparous young, suckled for a time by the mother, places them among the mammals, despite their fish-like form.

They converge in a remarkable manner toward the true fishes, notably the sharks; a second comparison lies with the ichthyosaurs, reptiles which occupied the same niche in nature's economy during the Mesozoic Era that the Cetacea do to-day, not only in general bodily adaptation to the seas but in their implied habits also. Yet another convergent group are the contemporary Sirenia or sea-cows, dugongs, and manatees, which, in spite of dissimilar feeding habits, were formerly included in the order of whales, as Cetacea herbivora in contrast with the Cetacea carnivora. Now enough is known of the Sirenia to place them entirely apart, for, as we shall see they are really sea-going ungulates derived from the same stock as that which gave rise to the proboscideans. Their only claim to relationship with the whales lies in their common heritage as placental mammals, and there the kinship ceases.

The actual nearest relatives of the Cetacea are the Carnivora, out of a more or less common creodont ancestry. Such evidence as we possess for this relationship will be set forth later.

Characteristics.—These are mainly specializations for life in the great waters and are many and varied.

The contour is typically that of a swiftly swimming fish, stream-lined, the head confluent with the body without a discernible neck. In but one or two forms is any movement of the head on the body possible. From the point of greatest girth about one-third of the way back from the snout the body tapers into the "small" from which the widely expanded flukes take their origin. These, in common with those of the sea-cows, form a horizontal

propelling fin of high efficiency, the two flukes being divided by a notch on the hinder border. They have no bone other than the centrally placed caudal vertebra but are supported by a dense fibrous connective tissue.

The head is relatively large, being sometimes one-third the total length of the animal. The gape is very wide, as the entire mouth has a prehensile function, the masticating portion common in mammals being absent. The lips are stiff and contain a great deal of oil.

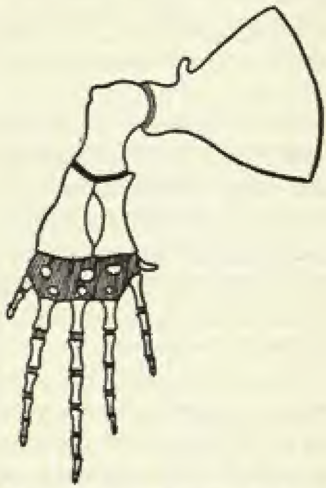


FIG. 181. — Pectoral limb of *Eubalaena australis*. (After Van Beneden and Gervais.)

The fore limbs, the "fins" or pectorals (Fig. 181), are ovoid paddles, freely movable at the shoulder but showing no external indication of digits or claws. The hand cannot be clenched, but the fin is somewhat flexible. It varies greatly in form and proportions in different whales. Its function is balancing and sometimes in part propulsion, also to aid in vertical and horizontal steering.

The hind limbs (Fig. 182) are vestiges, entirely within the flesh, and consist of one or more bones on either side, the ischia and sometimes a small femur, rarely a portion of the tibia as well. The actual limb bones are found only in the whalebone whales, with the exception of the cachalot (*Physeter*). In but one recorded instance out of thousands of captures has an external hind limb been seen. A humpback whale (*Megaptera nodosa*) taken off the Vancouver whaling station in July, 1919, possessed, on either side of the vent, a tapering cylinder about four feet two inches long containing a cartilaginous femur, a bony tibia, vestiges of the tarsus, and a metatarsal bone—a remarkable case of racial atavism.

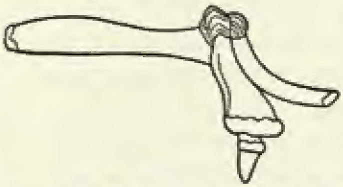


FIG. 182. — Pelvic bones of *Eubalaena mysticetus*. (After Van Beneden and Gervais.)

A dorsal fin, which varies in shape, height, and position, is present in most whales. It is absent, however, in the right whale and the white whale, and is vestigial in the sperm.

The skin is smooth and glistening, with no trace of hair, except for a few coarse bristles about the lower lip and sometimes around the blow-hole and forward to the snout in the sulphur-bottom. Even the fœtal hair is lost in the white whale (*Beluga*), showing how extremely long its aquatic adaptation has been. Hair is valueless as a heat-retaining clothing when submerged, for its principal efficiency lies not in the hair itself but in the static blanket of air which it contains. The replacement of the air by water is what nullifies hair as a non-conductor. Its function is taken by the blubber. This consists of a mesh of connective tissue, lying beneath the skin, and containing oil, which is fluid in the living whale but congealed in the dead animal. Blubber varies in thickness from one to three inches in the smaller porpoises to 17 inches or more in a fat sperm whale and is immensely tough, resisting strains up to thousands of pounds.

The eye is relatively small for the bulk but actually large in a great whale, up to four times that of an ox. It is situated not far from the hinder angle of the mouth—sometimes immediately behind it, again above. Some whales, like the sperm, are limited in the range of their vision—naturally they cannot look backward, nor can the sperm see forward. A whale is sometimes seen to erect himself in the water and slowly revolve to sweep the horizon and thus assure himself of the absence or whereabouts of his enemies. The eyeball is immovable and lacks the power of accommodation, moreover the vertical and horizontal curvatures of the crystalline lens differ, so that a whale sees poorly in the air, due to astigmatism and inability to focus or roll the eye. The eyes are fitted to withstand not only the varying pressures due to submergence but the impact of the seas in rapid swimming.

There is of course no external ear or pinna, except that it is said occasionally to reappear as an atavistic structure in the porpoise. The ear opening lies in the wake of the eye and is a mere slit in the skin in the California gray whale, *Rachianectes glaucus*, and in the humpback, while in the Greenland whale, *Eubalaena mysticetus*, it is a minute aperture not over a quarter of an inch in diameter, sometimes hardly discernible, and again entirely lacking. The meatus is entirely closed in baleen whales. As water carries

sound with about four times the intensity of air, the ears serve their purpose well enough but would be of little service in the air. The tympanic bulla, which is large and well-developed, acts as a sounding-box. The water vibrations, being transmitted through the tissues, set up corresponding vibrations in the bulla, from which they are communicated by the chain of ossicles to the inner ear. The typical cetacean bulla is found in all the whales, including the extinct zeuglodonts, showing that this device for hearing was acquired very early and is an indication of inter-relationship of the three phyla.

The nostrils or blow-holes are situated at the apex of the head, except in the cachalot (sperm), in which the single crescentic aperture is at the extreme forward end of the truncated head, the "noddle end" of the whalers. As it is on the left side, the spout is oblique. In the whalebone whales the nostrils are separate; in the toothed whales they unite to form one aperture. The closing mechanism also varies in each group but is highly effective. The sense of smell is apparently lacking, at any rate while submerged. Judging from the skull, the zeuglodonts must have possessed a fairly well-developed sense of smell for use on the surface, in the baleen whales the olfactory organ is present but doubtfully functional, while in the toothed whales it is entirely lost. The spout is specifically characteristic. What it consists of has been a subject of discussion, but it must be expired vapor from the lungs, because it dissipates into the air and does not fall back into the sea, as water would. It is comparable to that seen in our breath on a cold day, but in the whale it is visible at any temperature. If the whale begins to blow before the nostril has actually cleared the surface of the water, some of the latter will naturally be sent aloft with the force of the blast.

The duration of submergence naturally varies with the species and size (and age) of the whale, a cachalot being under for fifty minutes to an hour and a quarter. Returning to the surface the animal, if undisturbed, will blow 60 or 70 times with great regularity during a period of about twelve minutes. He then pitches head downward until he stands vertically with the flukes high in the air, and sounds to a great depth, possibly a half-mile to a mile. How he withstands the enormous pressure changes to which he is subjected is a mystery, for at the extreme depth the pressure would be nearly a ton to the square inch!

The skeleton is composed of light bone, the spongy cavities of which are filled with oil, and is rather simple in appearance compared with that of many land animals. This is due in large measure to the fact that the body is water-borne and the stresses are few, except for resistance to the longitudinal force of the huge muscles of the trunk and tail.

The skull, like that of many marine vertebrates, is peculiar in that the cranium is short and high, almost globular in some instances, while the jaws form a more or less prolonged rostrum or beak. All cetacean skulls above the zeuglodonts give indication of telescoping in differing degrees, and this has resulted in the shortening of the cranium; whales were evidently derived from a group of animals in which the sutures of the skull were squamous, that is, overlapping, rather than denticulate. Thus the bones can override and slip past one another. The telescoping, which differs in plan in the toothed and whalebone whales, is apparently the outcome of two opposing forces, one the resistance of the water and the other the forward thrust of the vertebral column, which have reacted upon the anterior and posterior portions of the skull respectively, each of which were plastic as compared with the more resistant middle area. In addition to this there is evidence of a downward stress in the whalebone whales, due to the form of the muzzle and the fact that, as they feed swimming with the wide mouth open, there is a tremendous downward drag to the jaws. The toothed whales do not show this, but in them the cranium is almost invariably asymmetrical (see Fig. 183) and apparently always in the same way, the vertex and condyles being shifted toward the left, as though they were subject to an oblique strain, due perhaps to the head being carried somewhat to one side; or it may be due to the fact that they do not swim in a perfectly straight direction, perhaps in part because of a sculling motion of the tail, just as the turning of a single screw propeller in one direction tends to deflect a boat from her course and has

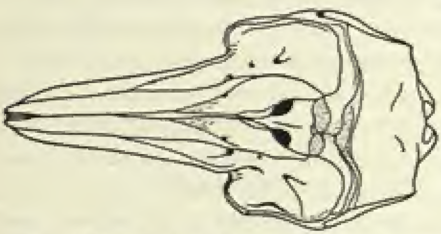


FIG. 183.—Skull of *Tursiops tursio*, showing asymmetry. (After Van Beneden and Gervais.)

to be offset by the helm. The telescoping and asymmetry are very ancient and were established before family differentiation arose. Both are apparent illustrations of kinetogenesis (see Chap. XII), but are, however, subject to hereditary control. The jaws of the baleen whales differ in contour from those of the toothed whales, being bowed upward or outward as the case may be; in the latter they are straighter and more parallel.

The vertebral column is simplified (see Fig. 56), especially in the articulation of the elements with one another, due, as has been said, to the absence of vertical strains. In some instances the zygapophyses fail to meet, the only articulation being at the centra. The spinous and transverse processes may be prolonged, especially in the after regions, for muscular attachment. The short neck has been mentioned, and, while it contains seven vertebræ, a number which, with extremely rare exceptions (tree sloths and manatee), is universal among mammals, the individual bones are extremely short and often coössify into a single bony mass, due to the same forces that gave rise to the telescoping of the skull. There is no present indication of a sacrum, although certain vertebræ just anterior to the caudals must represent such a structure historically. The lack of hip bones, other than the small flesh-buried ischia which have no connection with the vertebral column, has made for a secondary simplification of this region of the body, back to a primitive condition comparable to the fishes. The caudals are recognizable only by the presence of V-shaped chevron bones beneath them, which protect the great blood-vessels of the tail, as the neural arch protects the spinal cord. The posterior caudals are reduced to the centra alone and show a dorso-ventral flattening, corresponding to the horizontal expansion of the flukes. There are no bones supporting either the flukes or the dorsal fin. The ribs are also simple, generally single-headed, and usually but one (Mystaceti) to four or five (Odontoceti) articulate with the sternum. In the pygmy right whale (*Neobalæna*), all but the first three or four ribs have actually lost their connection with the vertebræ themselves. There are no clavicles, and the scapulæ have a very characteristic form, generally fan-shaped, though differing characteristically. The head of the humerus is spherical and freely movable within the shoulder socket, all of the other articulations of the fore limbs being imperfectly formed, so that no bending of the joints is possible other than a certain flexibility of the entire

fin. All of the bones beyond the humerus are flattened and often, especially in the carpus, are widely separated by cartilage. Sometimes in old whales the wrist bones fuse into a single element. The digits are generally five in number, although the first may be lacking and one or two others reduced. The whalebone whales have lost the thumb which the toothed whales have retained. The second and third digits and sometimes the fourth may exhibit hyperphalangy, especially in such a whale as the humpback (*Megaptera*, Fig. 193) in which the fins are very long.

The teeth vary greatly in their development. Disregarding for the time being the ancient aberrant whales, the zeuglodonts, the teeth are generally reduced to compressed cones, each with a single root, and have increased in number greatly beyond the primitive 44 of the placental mammal, for a modern dolphin may have upwards of 250 teeth. The teeth may be present and functional in both jaws, as in the porpoises, or in the lower jaw only with vestiges in the upper gums in the sperm whale (*Physeter*). They may be reduced to a single pair of strap-like teeth in the lower jaw (cow whale, *Mesoplodon layardi*, Fig. 184), or to a single long upper tusk, as in the male narwhal (*Monodon*). In the whale-bone whales (Mystacoceti) functional teeth are utterly lacking, but small pin-shaped vestiges are present in the embryo, buried in the gums. These soon disappear entirely. (A further description of the mouth armament will be found under the several genera discussed.)

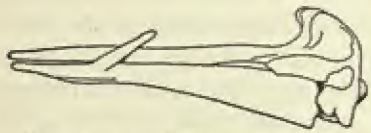


FIG. 184. — Skull of *Mesoplodon layardi*. (After British Museum Guide to Whales.)

The milk glands open on either side of the vent and are provided with reservoirs with compressor muscles which contain an abundant supply of rich milk. This accelerates the feeding of the young.

In size the Cetacea vary enormously from perhaps $2\frac{1}{2}$ feet in the smaller porpoises to 90, 100, or even 110 feet for the great blue whale. For a whale of 75 feet the weight approximates a ton to the foot, but as the bulk increases with the cube the greatest weight may run up to 150 tons: by far the largest animal that lives or has lived, for no dinosaur known had a comparable tonnage. (See Fig. 64.)

In agreement with most creatures which depend upon movement for safety, the young are mentally precocious.

Habitat.—Cetacea inhabit all the known seas; some are cosmopolitan, others restricted in their cruising range. Yet others, normally marine, may ascend certain tidal rivers, while certain of the dolphins are exclusively confined to fresh water such as the larger rivers of South America, the Amazon, La Plata, and Orinoco, as well as the Ganges, Irawaddy, and Chinese rivers of Asia.

Habits.—While all Cetacea are carnivorous animals, but two genera, *Orcinus* the killer whale (Fig. 57) and *Pseudorca* the lesser killer, feed upon warm-blooded prey—seals, penguins, and other Cetacea. The killers acting as a pack will make a concerted attack on the Greenland whale and tearing open the lips devour out the tongue, which effectually decommissions the victim even though he may not die directly as a result of the injury. The other toothed whales feed upon fishes, but especially upon crustaceans and cephalopod mollusks. This last is particularly true of the cachalot, learned not only from direct observation but from the stomach contents which the whale disgorges in his death flurry.

The baleen whales on the other hand feed upon small planktonic organisms such as pteropod mollusks or sea-butterflies, and Crustacea, thousands of which are sacrificed for a meal. The method of their feeding will be detailed later.

In habits other than feeding, whales are gregarious and were formerly found sometimes in schools of many thousands, others singly or in pairs, but the numbers are now sadly diminishing, owing to intensive steam whaling. Individually they are timid and inoffensive, except when the young are threatened or injured and maternal solicitude comes to the fore. The male cachalot is occasionally aggressive, and while some can be killed with little protest, others are fighters and not only turn upon and smash the boats with head, flukes, and jaw but have been known to sink the whale ships themselves. Among recorded instances are the "Alexander" and "Kathleen" of New Bedford, the latter in 1902 being charged repeatedly until she opened up so that she sank. A more terrible tale is that of the "Essex" of Nantucket in 1819, involving the grimmest of deep-sea horrors before her men were finally rescued. The "Essex" met a whale head-on when each was making about three knots. The ship began to leak, while the whale withdrew to a distance of about a mile. When he had recovered

from the concussion he charged the ship, staving in her bow so that she sank in five minutes. How many of the other missing whale ships during the long years of the industry owe their destruction to whales no one can say. In general, however, the danger of the whale fishery is not due to offensive tactics on the part of the creatures themselves but to close contact of a small light boat with the huge bulk of a thrashing whale.

Evidences of Evolution

Ontogeny.—Occasional whale embryos are found within the mother and show several items of interest, such as the absence of flukes on the tail of the very young specimens—the flukes making their appearance later as lateral outgrowths of the tail. It was formerly thought that these possibly represented vestiges of the external portion of the hind limbs which had migrated aft from their normal position on either side of the vent. This is, however, disproved by the presence of external hind limb vestiges in the embryos in certain genera, such as *Megaptera*, which later disappear, and also in the specimen of *Megaptera* mentioned above, in which the atavistic hind limbs were present in addition to the flukes.

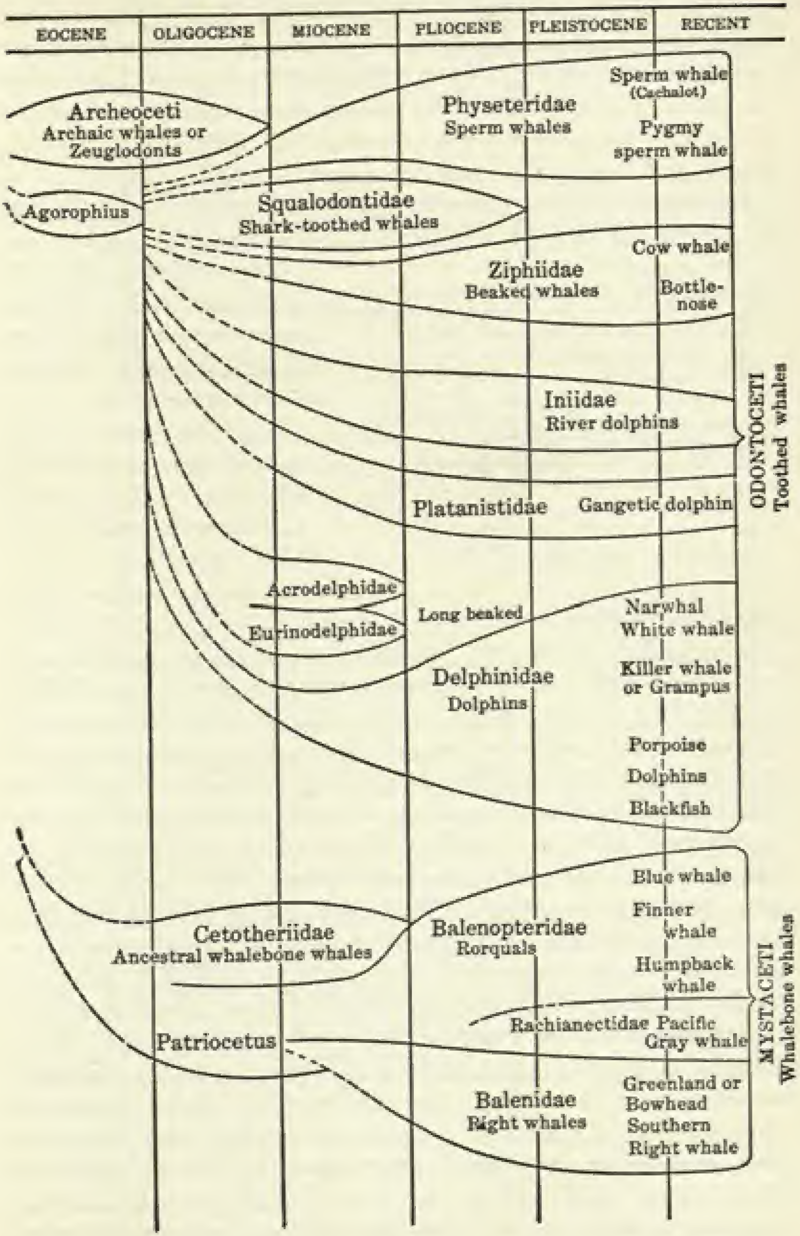
The angulation of the head on the neck in the normal quadrupedal posture is another interesting feature shown by the embryo whales.

In the baleen whale embryos, "as many as forty or even more minute teeth with pin-like crowns may be found hidden in the gum on the maxillary, but they are soon resorbed. The atrophy of the teeth is followed by the growth of papillæ along the outer margin of the upper jaw and these develop into a series of crosswise-placed corneous [horny] blades, the baleen" (Tullberg [1883] from Kellogg [1928]).

Systematic Review

Whales are divided systematically into a number of phyla, of which the three principal ones are (1) the Archæoceti, aberrant Eocene whales which died out without further issue toward the close of the Oligocene. Out of some primitive forms, as yet unknown, however, arose the later whales which in turn are divided into (2) the Mystaceti or baleen whales whose vestigial embryonic teeth point to a toothed ancestry, and (3) the Odontoceti

PHYLOGENY OF THE CETACEA



or toothed whales. The last are again divided into three or four families: the Platanistidæ or river dolphins; the Delphinidæ including the porpoises, sea dolphins, killers, and perhaps the narwhal and white whale (*Beluga*), (although by some these are put in a separate phylum), finally the Physeteridæ, cachalots or sperm whales and the pygmy sperm (*Kogia*); the Ziphiidæ or beaked whales; and the Iniidæ which are largely extinct.

Archæoceti.—These aberrant whales are confined entirely to the Eocene and Oligocene epochs, first appearing in the rocks of the Lybian desert, Egypt, and culminating in bizarre types from the Gulf States of the United States of America.

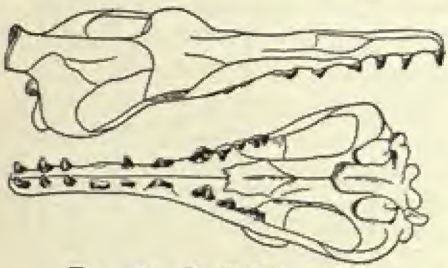


FIG. 185.—Skull of *Protocetus*. (After Fraas.)

The first known form is *Protocetus atavus* (Fig. 185) from the Lower Mokattam series near Cairo. This form serves to link up these whales with their land-dwelling ancestry, for it combines features of the creodonts, especially in the teeth, with the typical skull of a zeuglodont.

The next genus, both in stratigraphic occurrence and degree of evolution, is *Prozeuglodon*, intermediate in character between *Protocetus* and *Zeuglodon* proper. The peculiar features of the skull and teeth can best be seen in the final phase, *Zeuglodon* or *Basilosaurus*. Distinctive features of *Prozeuglodon* (Fig. 63) are an elongated skull, the cranium of which has not yet taken on the telescoped character of the later whales. The anterior nostrils have receded to a position a little more than one-third the way from the muzzle, and the zygomatic arch tends to lighten as compared with a creodont skull. The teeth are peculiar, those of the forward half of each jaw being simple, somewhat curved cones, as in the later whales, while the cheek teeth are two-rooted with a laterally compressed crown which in the premolar teeth has a characteristic serrated appearance on both margins. The molars may be similar or their anterior margin may be plain, the serrations being confined to the posterior only. These teeth are apparently an adaptation for the holding and shearing of slippery prey and are somewhat similar to those of certain seals of supposedly comparable

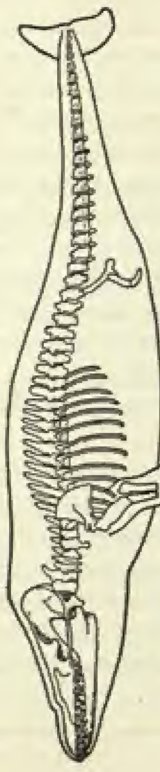


FIG. 186.—*Zeuglodon osiris.* (After Abel.)

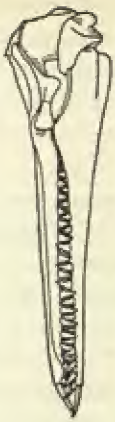


FIG. 187.—Skull of *Squalodon.* (After Stromer.)

FIG. 188.—Cachalot, *Physeter catodon.* (After Scammon.)

feeding habits. The proportions of *Zeuglodon osiris* (Fig. 186) of Egypt are more like those of most whales, while *Basilosaurus cetoides* of Alabama is immensely elongated, especially in the lumbar vertebræ, and has a total length of 50 or 70 feet. The short-bodied zeuglodonts were of the proportions of an ordinary whale and like them must have swum with the up and down motion of the tail. The elongated types, *B. cetoides* and *isis*, must have lashed the entire body in a serpentine manner, aided of course by the flukes. They were probably much less efficient and speedy than their more compact relatives. *Basilosaurus* converges strongly toward the reptilian sea lizards or mosasaurs (see p. 300, Fig. 62) of Cretaceous time and is the final expression of zeuglodont evolution, for with this genus, except for a few smaller Oligocene survivors, the entire line of Archæoceti becomes extinct, as these later forms have no connection with existing whales.

Odontoceti.—This phylum embraces all of the toothed whales and dolphins other than the zeuglodonts and includes several divergent families which agree, however, in general conformity to type, the main distinctions being chiefly confined to the head and dentition. The structural ancestors, if not the actual ones, of the toothed whales belong to the family Squalodontidæ, shark-toothed dolphins. These have a very full dentition, the anterior teeth being conical and single-rooted, while the posterior ones are two- or three-rooted with a compressed serrated crown.

The oldest of the Squalodontidæ is the small *Microzeuglodon* from the Caucasus, referred to Eocene time. The teeth and humerus alone are known, but *Squalodon* (Fig. 187) is well represented in the Miocene of continental Europe. The beak is long and slender, much more so than in the related *Prosqualodon* of South America.

From the Squalodontidæ arise the sperm whales, Physeteridæ, the intervening types, according to Abel, being *Scaldicetus* from the Miocene and Pliocene of Europe, North America, and Patagonia, the finely serrated teeth of which are single-rooted; *Physeterula*, Miocene of Europe, in which the teeth have lost their enamel; *Prophyseter*, in which the upper teeth are gradually lost, the incisors early in youth, the maxillary teeth later; and *Physeter* itself. The last mentioned, toothless in the upper jaw, first appears in Pliocene time. The actual evolution of the family occurred during Miocene time, with little change since.

The modern sperm whale or cachalot (*Physeter catodon*, Fig. 188), is of remarkable aspect with a huge blunt head, which is at least one-third the entire length. The skull within is most peculiar, with a large curved transverse crest and slender upper jaws which serve to support the "case," a reservoir of liquid oil known as spermaceti, and the spermaceti cushion. The cervical vertebræ are fused with the exception of the atlas. The sperm whale's lower jaw is also slender and is armed with two nearly parallel rows of 20 to 25 gleaming teeth, each of which is a stout, somewhat recurved cone of a good quality of ivory. There is a very low dorsal fin of irregular outline, and the pectorals are rather small.

The color is black above, shading into gray below. The food consists largely of squid, especially the giant squid, *Architeuthis* (Fig. 110), to capture which the whale must dive deep, probably down to the twilight zone of the sea, and therefore suffer a very great increase of pressure. The single blow-hole of this whale is not at the apex of the head but at the end of the blunt snout and on the left side, so that the spout is characteristically oblique. Cachalots are among the larger of the whales, ranging from 50 to upwards of 65 feet. They are fairly fast swimmers, making five to six knots, probably more when excited. The diving speed is eight knots. The sperm whale is one of the most widely distributed of all, inhabiting for the most part the warmer seas but venturing as far north as the Shetland Islands. This together with the right whale was the one most sought for by the old-time whalemen for the high value of its oil, especially the spermaceti.

Another available product of the cachalot is the substance known as ambergris, an intestinal secretion due apparently to the irritation caused by the beaks of the squid which form its food. Occasionally an emaciated whale will contain the material in its intestine, at other times it is found afloat. Its value of \$15 to \$20 an ounce is due to its demand as a basis for perfumery, in that it has the peculiar property of intensifying greatly any other perfume with which it is compounded. In 1898 a lump of 270 pounds sold in Paris for £18,360 or about \$89,000. It is not in itself pleasant but had formerly a supposed medicinal value.

The pygmy sperm whale (*Kogia*) is the only other living member of the Physeteridæ. It is from 9 to 13 feet in length.

Another family of whales is the Ziphiidæ, or beaked whales, in

which the functional teeth entirely disappear, except for one or two pairs in the lower jaw. There are, however, vestigial teeth which do not cut the gum. Like the sperm whales, the beaked whales complete their evolution by Upper Miocene time, an immediate ancestor being *Cetorhynchus*, preceded by *Diochotichus* of the Lower Miocene, the earliest recorded ziphioid whale. The principal living genera are *Mesoplodon*, the cow whale, *Ziphius*, and *Hyperoödon*, the latter the bottle-nose. *Mesoplodon* has persisted from the Upper Miocene, although now diminishing in numbers. There is but a single pair of lower teeth, which in *M. layardi* (Fig. 184) curve upward and inward in such a way that in old individuals they meet above the upper jaw, apparently limiting the opening of the mouth, a specialization of doubtful value to its possessor. *Hyperoödon*, the bottle-nosed whale, is rather small of head, with large maxillary crests greatly developed in the male. This whale, which may be 30 feet in length, is black in the young and grows lighter with age. Its submerged depth and endurance are great, two hours being recorded. Another peculiarity mentioned by Beddard is that it "can leap right out of the water, and while in the air can turn its head from side to side," an accomplishment known of no other whale. *H. rostratum*, the common bottle-nose, is found in the northern seas. They are said to "sob" in their vocalizations. They are gregarious, the school or "gam" numbering four to fifteen.

Eurinodelphidæ. This family of whales are numbered among the extinct at present but in Miocene time, especially in Belgium and North America, they were the most abundant of all that have been preserved to us. They are characterized by an immensely prolonged and very narrow rostrum, which is thrice the length of the cranium, and in which both jaws possess numerous simple teeth. *Eurinodelphis* is the principal known genus, which partakes of the nature of both the beaked whales and the dolphins. They are evidently related to the Ziphiidæ, although forms directly ancestral to the latter are as yet undiscovered.

Iniidæ. The rostrum is long in the more primitive genera but later somewhat shortens; the numerous teeth, with the exception of those in *Inia* itself, are simple single-rooted cones. The cranium is rounded and the cervical vertebræ distinct, the other vertebræ being elongated.

Inia has a vestigial dorsal fin and large ovate pectorals, and the

posterior teeth often bear an accessory tubercle. The skull lacks the high maxillary crests of *Platanista* (Fig. 190), and the vertebral column is short, having but 41 vertebræ. The neck vertebræ, on the other hand, are rather long for a whale. The single species, *Inia geoffroyensis*, is a native of South America, inhabiting the Amazon River. It varies in color from pink to black above and pink below and is held in superstitious dread by the natives, who claim that it will attack them; while *Sotalia*, a true dolphin (yet to be described), will defend them from *Inia*. *Inia* reaches about seven feet in length. *Pontoporia* (Fig. 189), the La Plata dolphin, has a well-developed dorsal fin and a long rostrum with 50 to 60 pairs of teeth, 200 in all. This creature has a color corresponding closely to that of the water, brown with some variations. It is smaller than *Inia*, measuring but four feet in length. *Pontistes*,

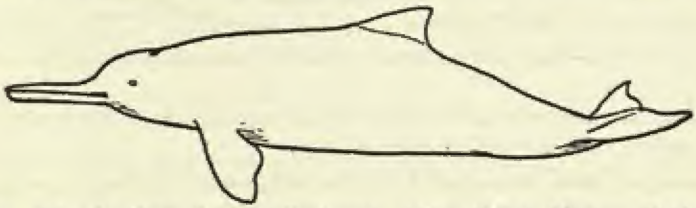


FIG. 189.—La Plata dolphin, *Pontoporia*. (After British Museum Guide to Whales.)

an extinct Argentine genus, resembles *Pontoporia* closely but exceeds it in size. The toothless extremity of the mandible turns up, which is an absolutely unique feature. Other Tertiary genera, *Pontivaga* and *Ischyrorhynchus*, are also known from Patagonia and Argentina, while *Cyrtodelphis* is an abundant fossil in the Miocene of Europe and North America (Abel).

Platanistidæ. This is the first family of river dolphins to be considered, the susa, *Platanista gangetica* (Fig. 190), inhabiting the Ganges, Indus, and Bramaputra rivers of India. It also has a fairly long beak with thin sharp teeth, which grow thicker and blunter with age. The skull bears a high crest. The peculiarity of this eight-foot whale lies in its blindness, as the muddy rivers and its habit of groping in the bottom mud for the crustaceans and fishes which form its food render sight of little value.

Delphinidæ. This is by far the largest family of whales but does not include the largest individuals, for these are the dolphins and porpoises of small to moderate size. As a rule there are

numerous teeth present in both jaws, and the skull never shows the large maxillary crests of the Iniidæ. As many as 19 genera of Delphinidæ with some 50 species have been described, grouped into at least two subfamilies. Of these the first is Delphinapterinæ

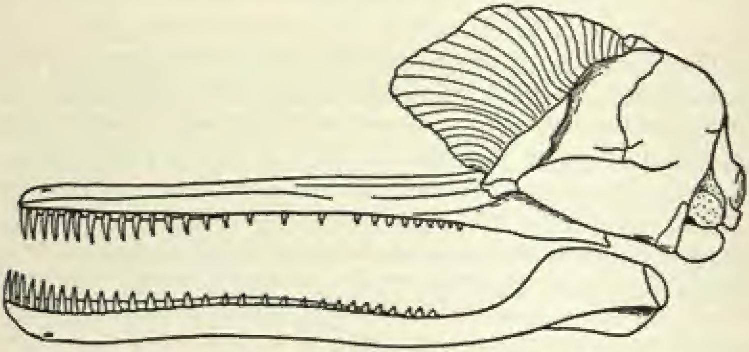


FIG. 190.—Skull of *Platanista*. (After Van Beneden and Gervais.)

(Beluginæ), including the white whale, *Beluga*, and the narwhal, *Monodon*, with a single species of each.

Beluga (Fig. 191) is a northern whale about 10 feet in length, white in color as an adult, although blackish when young. Its head is rounded, and there is a distinct constriction of the neck, as in the Platanistidæ, with a corresponding lack of coössification of the neck vertebræ. This creature, while marine in distribution, will occasionally ascend the rivers in search of food, being especially

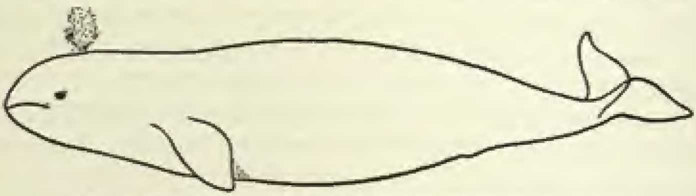


FIG. 191.—*Beluga*, the white whale. (After Scammon.)

fond of salmon. It has comparatively few teeth, eight or ten, in the anterior part of the mouth, and there is no dorsal fin.

The narwhal, *Monodon*, is unique among whales in the possession of a tusk or horn, developed in the male, vestigial in the female. This is the continuously growing upper incisor tooth, generally the left, sometimes the right, rarely both, which is a

spirally twisted horn of ivory, the twist always turning to the left, whether the tusk be left or right. Aside from the tusks, these whales are entirely toothless. In other respects the narwhal agrees closely with *Beluga*, although its color differs in that it is generally spotted, though older animals also tend to become white. The horn is of course a secondary sex character and is difficult of explanation. Its use as a weapon for the combat of rival males seems hardly convincing, for, although they have been seen to cross tusks as though fencing, they seem to be gentle animals, as are most whales, and I know of no record of an actual conflict. Another suggestion is that the horn may be used to break and maintain blow-holes in the thick ice of their arctic home. If so, why do not the females possess them, unless the males are sufficiently gallant to provide free air for both sexes? Their suggested use as a weapon in impaling their prey is also apparently without proof. It is of interest to students of heraldry that the narwhal's horn is that of the fabled unicorn, which supports the British coat of arms. The tusk was supposed to have medicinal properties during mediæval times. Narwhals are rather small, seldom exceeding fifteen feet, not including the tusk, which may be seven feet or more in length. Like the white whale, the narwhal is hairless, even on the lips. It is said that the embryo beluga is devoid of the usual fœtal hair. Whether this is also true of the narwhal is a question. The food of the latter is largely molluscan, with some fish.

Subfamily Delphininæ, the dolphins and porpoises. These are comparatively short-snouted forms with a well-rounded cranium. The teeth vary in number in both upper and lower jaws but are simple single-rooted cones. There are no teeth in the premaxillaries, but as the maxillaries extend to the end of the upper jaw the teeth are well distributed. The anterior cervicals are fused. At present this subfamily includes the greatest number of living toothed whales. They are very widely distributed, inhabiting not only the seas but the mouths of some rivers, although rarely exclusively fluviatile. Fossil dolphins range from the Lower Miocene on but are relatively not so numerous. Certain of the family, notably the harbor porpoise, are found occasionally with what appear to be dermal ossicles and have been taken as evidence for the derivation of this group of cetaceans, if not all of them, from an armored ancestry such as the edentate stock. Other

authorities claim that the so-called ossicles are merely calcifications of the skin and have arisen as new structures, having no historic significance. Certainly there is little other evidence for an edentate ancestry, and no other group of mammals are known to possess such an exo-skeleton. There seems to be no valid reason for supposing that the dolphins have arisen from a different ancestry from that of the other Odontoceti, although they have been an isolated group since Lower Miocene time.

Delphinus (Fig. 192). This genus includes the common dolphin, *D. delphis*, which has a more distinct beak than most of the other forms. It varies so much in color and proportions, including the

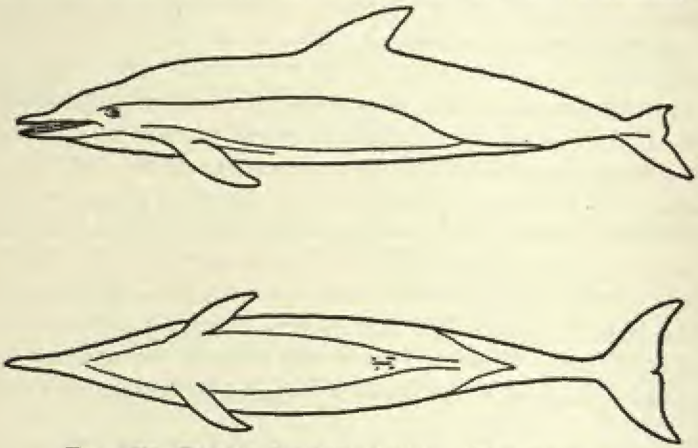


FIG. 192.—Dolphin, *Delphinus bairdii*. (After Scammon.)

numbers of teeth, that it has been divided into as many as seventeen species; this, however, seems to be without adequate foundation. The small teeth may number as many as 65 pairs. Of the cervicals only the atlas and axis are fused, the pectorals are somewhat sickle-shaped (falcate). This is the dolphin so conspicuous in the storied traditions of the past and in heraldry and coinage, where it is usually represented with arched back, as it generally appears when rounding out to breathe. The genus *Sotalia* is also beaked, but its teeth are larger and fewer. It differs from the other Delphininæ in being largely restricted to fresh-water. One in the Amoy River of China is nearly white in color, that in the bay of Rio de Janeiro is pale brown. Most remarkable of all is *S. teüszii* from the African Cameroon River, which not only has an ex-

ternal tubular blow-hole, but is said to be vegetarian in its feeding habits. This last is borne out by the stomach contents of one individual, but whether it is universal with the species is not clear.

Tursiops is represented by *T. tursio*, a very widespread dolphin. It is black to lead color above and white beneath.

Tursio is distinguished from *Tursiops* by the absence of a dorsal fin. The latter is known from Pliocene time.

Phocena, the porpoise, has a row of tubercles along the dorsal fin; it is also blunter headed than *Tursiops* and lacks the distinct beak. *P. communis* ranges from 6 to 8 feet in length and in it six cervical vertebræ are fused. It is gregarious, often following ships, and will ascend rivers.

Globicephalus has its teeth reduced to 7 to 12 pairs, and the head is peculiar in form, rising sharply behind the nostril, hence the name. This whale also lacks a beak. Its length of 23 feet makes it the largest of Delphinids, and its great numbers and sheep-like herding instinct make it easy of capture. The popular name of the most familiar form is pilot whale or ca'ing whale. Another distinctive character is the degree of hyperphalangy of the two middle digits of the hand, as many as 12 to 14 bones being present in each. (See Fig. 13,C.)

Grampus is another allied genus. There are 3 to 7 teeth in front of the lower jaw, but none above, a condition comparable to the sperm whale and rare among the dolphins. There is again no beak, and the pectorals are long. It is not a very common whale.

Orcinus orca (Fig. 57) is one of the most interesting of the dolphins. It is the killer whale and is often, though erroneously, known as the grampus. The killer is a powerful creature, sometimes 30 feet in length, and is black with conspicuous markings of white and yellow. It is, as we have seen, the only cetacean to prey habitually upon warm-blooded creatures. It has a high, pointed dorsal fin which adds to its striking appearance. Its voracity may be measured by the stomach contents of one specimen, which consisted of 13 porpoises and 14 seals! We have told of the combined attack of these sea-wolves upon the huge but comparatively inoffensive Greenland whales. The offensive weapons of *Orcinus* are its strong conical teeth, upwards of 42 in number.

Pseudorca differs but little from *Orcinus*. The teeth are fewer and the dorsal fin smaller and nearly all of the cervicals are fused—

twice as many as in *Orcinus*. *Orcella*, another allied genus, is both marine and river-inhabiting (Irawaddy). *Pseudorca* was first known as a fossil from the Pleistocene of the Cambridge fens. It was not until later that it was found to be living.

Mystaceti or baleen whales.—These are the whales in which the teeth are embryonic germs only, their function being subserved by the whalebone or baleen which hangs from the roof of the mouth. As a rule, the upper jaws are slender and are bowed upward in varying degree, while the lower jaws curve outward in the horizontal plane, touching at the anterior end without actual fusion. Between them is the huge tongue, a vital part of the food-getting mechanism to be described.

In contrast to the Odontoceti the skull is perfectly symmetrical and the blow-hole a paired aperture. The ribs are always single-headed and articulate with the transverse processes of the vertebræ only. With but a single exception, the pygmy right whale, *Neobalæna*, the whalebone whales are vast animals, being equalled among the Odontoceti only by the sperm whale, *Physeter*. Some of them exceed the ponderous proportions of *Physeter* itself, for the great blue whale, *Balaenoptera*, with its upwards of 110 feet of length, belongs here. (Fig. 64.)

The feeding mechanism consists of triangular plates of a horny substance, baleen, which hang from the roof of the mouth, comparable to the transverse ridges which many mammals bear on the palate. These are frayed out into a hair-like fringe on their inner edge. So numerous are the plates that their combined fringes form a veritable sieve which permits nothing but water to pass between them. The whale, with the mouth wide open, rushes through vast swarms of small floating organisms (chiefly planktonic Crustacea and mollusks, like the sea-butterflies or pteropods). It then closes the mouth and presses the great tongue upward, thus driving out the water. The food, left stranded upon the tongue, is then swallowed. The plates of baleen vary in length and number in different whales, reaching a maximum of 370 with a length of 13 feet in the bowhead. Their color varies according to the species from black through pink to white. In 1897 whalebone was valued as high as $10,000 a ton, and a single whale might produce several tons. To-day, owing to changing feminine styles and the advent of the automobile, there is no market for it, as its principal use was for corsets and buggy whips!

There are three existing families of Balænids, the Balænopteridæ or rorquals, the Rachianectidæ or Pacific gray whales, and the Balænidæ or right whales.

Balænopteridæ. These are the largest of whales, although as a rule relatively less bulky than the Balænidæ. The other distinguishing features are the grooved or furrowed throat and the presence of a dorsal fin. The bones of the comparatively smaller head are not so highly arched, and as a consequence the baleen is shorter. The furrowed throat seems to be a partial compensation for this, as it permits of greater expansion and consequent movement of the tongue so that the feeding mechanism is just as effective. There are but four digits in the hand, as compared with five in the right whales, and the seven cervicals are not fused. The most interesting of the rorquals are the finner, blue, and humpback whales. Of these the finner (*Balænoptera velifera*) ranges from 44 to 67 feet in length, brownish black to black above, white beneath. The dorsal fin is high, and the pectorals relatively small. The number of baleen plates is about 330 on each side, and it feeds largely on small copepod Crustacea.

The blue whale or sulphur-bottom, *Balænoptera* (or *Sibbaldus*) *musculus* (see Fig. 64), is the largest of whales, specimens having reached the length of 100 feet and over, with an estimated weight of upward of 150 tons, by far the largest mass of animated flesh the world has ever seen, for if any of the sauropod dinosaurs approached it in length, and this is possible, their weight could not have been half as great because of their compact body and slender neck and tail. The common rorqual, *B. physalus*, is from 65 to 85 feet and the Sei whale not more than 50. All of these great whales are somewhat underpowered, their speed not exceeding 8 to 12 knots, although, as their conformation would imply, they have twice the speed of the stockier right whales, which is one reason why they were not pursued by whalers in the days of sail. Moreover, the short inelastic whalebone and relatively thin blubber rendered them far less profitable even if they could be overtaken. Modern steam whaling has changed all this, and the rorquals are no longer exempt from destruction.

One of the most amusing of whales is the humpback (Fig. 193), *Megaptera boöps* (or *nodosa*), a veritable clown, not only in appearance but in behavior. It is a large whale of 50 feet or so, stocky, with enormous pure white pectorals, which are about one-fourth

the over-all length of the animal. The fins are tubercled along their margin, as are the jaws and head. Humpbacks are very subject to parasites, especially whale barnacles, of which some other whales are comparatively free. As with the other rorquals, the throat is furrowed. The rather low, irregular dorsal fin is said to have given them their vernacular name; others claim that it refers to their habit of humping themselves when they emerge. They are widespread in all oceans and were once very numerous, but their friendliness and sportive habits have made them an easy prey to whalemen, so that their numbers are sadly depleted. The whale-bone is comparatively short and is black in color.

Rachianectidæ. This family includes a single form, *Rachianectes glaucus*, the Pacific gray whale. It differs from the rorquals in lacking a dorsal fin and in the reduction of the throat furrows to two or four. In size it is relatively small, but 40 to 50 feet, the color is a mottled gray varying to black, and the light-colored baleen is short. These are shore-loving whales, lying in the surf in two fathoms or so of water and often being held stranded until released by the succeeding tide. The capture of these whales in shallow water was a very dangerous business, due to "the quick deviating movements of the animal, its unusual sagacity." This is especially true of the females accompanied by their young, for they do not hesitate to chase, attack, and destroy the boats, thus endangering their crews, the resultant casualties to life and limb being frequent.

Rachianectes is the least modified of all the whalebone whales and is readily derivable from the ancestral cetiotheres. They have been spoken of as "living fossils," a term often applied to persistently primitive forms.

Balænidæ, right whales. These whales are at once distinguished by the disproportionately large size of the head, both in length (being one-third the over-all dimensions) and in height. The throat lacks entirely the furrows found in the rorquals. In spite of their enormous bulk, they rarely exceed 50 feet in length, and there is no trace of dorsal fin. They possessed in large measure the old-time requisites, an abundant yield of oil and very fine long whalebone, which gave them their popular name of right whale in contradistinction to the other Mystaceti, which were *wrong* from the point of view of profitable whaling.

There have been several genera and many species of these right

FIG. 193.—Humpback whale, *Megaptera boöps*. (After Scammon.)

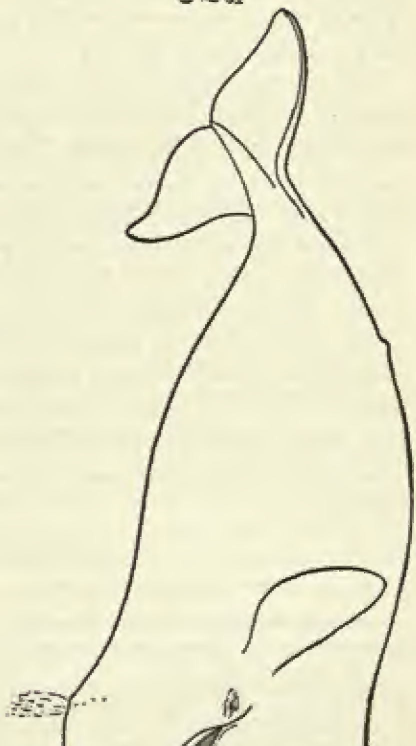


FIG. 194.—Bowhead or Greenland whale, *Balæna mysticetus*. (After Scammon.)

whales described, based either upon fragmentary material or upon variable individuals. As a matter of fact there are relatively few species and probably but one genus, *Eubalæna*. The Greenland whale is *E. mysticetus* (Fig. 194) and is confined to the Arctic Ocean, a timid, inoffensive type, which, however, dives to a great depth and is frantic in its efforts to rid itself of the harpoon—efforts which may result in a swamped or stove boat. All of this added greatly to the danger of old-time whaling, in addition to the perils of arctic navigation. The arctic whale is black with a white area on the under side of the jaw.

The southern right whale is *Eubalæna australis* (or *glacialis*) and seems to include all others the world over, but its range does not intrude upon that of *mysticetus*. The specific contrasts lie chiefly in the fact that in *mysticetus* the head is relatively larger and the whalebone longer and finer. Minor skeletal contrasts are also recorded.

Neobalæna is the pygmy whalebone whale, bearing the same relationship to the great whales that the pygmy sperm, *Kogia*, does to the cachalot, *Physeter*. Its length is but 20 feet. The dorsal fin is rorqual-like, but the shape of the head and absence of throat furrows, together with the long whalebone, link it rather with the right whales. The one species, *N. marginata*, is very local in its distribution, being found only about New Zealand and South Australia.

Ancestrally the whalebone whales are out of the Miocene Patriocetidæ.

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CHAPTER XXXV

PROBOSCIDEANS

Aside from the whales and the great dinosaurs of the Mesozoic, the elephants lead the animal kingdom in size and majesty, and stand unique in nobility of physical and mental characters. Add to this the fact that their evolution since the close of the Eocene can be traced with great fullness, and their claim to our interest, second only perhaps to that of the horses and mankind, is complete.

Place in Nature.—The placental mammals may be grouped, principally according to the character of their foot armament, into four cohorts: the clawed or unguiculate forms, the hoofed or ungulate, the nailed or primate, and the cetaceans or whales. Of these the Carnivora, as representatives of the unguiculates, and the whales have been discussed, and we now pass to a consideration of the hoofed creatures, of which the Proboscidea form, in a sense, one of the most primitive of living orders.

Proboscidea are therefore members of the class Mammalia, cohort Ungulata, which embraces also the familiar Perissodactyla and Artiodactyla, the archaic Condylarthra and Amblypoda, and the curious South American ungulates, as well as the Hyracoidea, and, as an appendix to the cohort, the Sirenia or sea-cows. It is with the last two orders particularly that we are concerned, for Paleontology has shown that however far removed from the lordly elephant the humble hyraces or conies on the one hand and the whale-like sea-cows on the other may be, they are nevertheless the nearest to the Proboscidea of all mammalian orders.

The great divergences between the ultimate representatives of the Proboscidea and Sirenia, the elephant and manatee, are merely due to environmental adaptation, the offspring of swamp-dwelling ancestors coming to a parting of the ways of which one leads to firmer ground, the other to the waters. The elephants' evolution, as we shall see, largely concerns the head; the body, except for the increase in bulk and the mechanical readjustment of the limbs to bear the weight, exhibiting but little change with the flight of time.

The sea-cow (Fig. 195), on the other hand, is profoundly altered in its body contour, the hind limbs have disappeared, and in their stead there has been developed a propulsive tail. The head, however, in contrast with that of the elephant, has remained practically as it was.

FIG. 195.—Manatee, *Manatee australis*. (After Brehm.)

ELEPHANT ANATOMY

Something of the anatomical structure of the elephant is necessary to an understanding of the evolutionary changes which its ancestors have undergone. In our discussion of this structure we will speak first of the primitive or archaic characteristics, then of the elephant's specializations.

Archaic Characters

The elephant contains within its huge body a number of primitive features, for the soft parts of an animal's anatomy, with the exception of the skeletal muscles, are less subject to mechanical stresses and are therefore rather more conservative in their rate of change than are the bones and teeth. To enumerate briefly: the stomach is simple in form, the liver has but two lobes without a gall-bladder, the lungs are simple and but slightly lobated, there are two superior venæ cavæ (the ancient number) which carry blood to the heart, the placenta by which the unborn young are

nourished is primitive, and finally the brain, although huge in size, is old-fashioned in form in that the cerebrum or fore-brain does not cover the cerebellum, a notable contrast with that of man.

Skeletal Structures.—The feet are five-toed, although there is a tendency toward the reduction of the lateral digits of the hind foot, especially in the African elephant. The number of hoofs may be fewer than the actual digits, as the entire structure is encased within a huge cylindrical mass of flesh and skin so that no external sign of the digits other than their terminal nail-like hoofs is visible.

The carpal or wrist bones are serial, that is, placed one above another in line with the metacarpals themselves. This is the type of wrist seen in the condylarth *Phenacodus* (Fig. 170) as compared with a displaced or interlocking carpus in which the bones alternate as do the stones in a well laid wall.

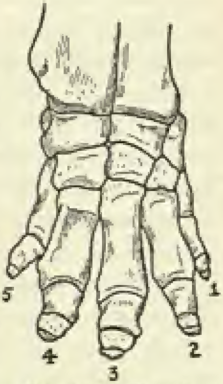


Fig. 196.—Fore foot of elephant, *Elephas maximus*, viewed from in front, showing the serial carpals or wrist bones. (After Flower.)

On the part of all cursorial ungulates such as the horse or deer the ulna tends to reduce, especially in its lower two-thirds, the upper portion, which forms the elbow joint, being of necessity retained. In the Proboscidea, on the other hand, not only is the ulna retained entire, but it has become the dominant bone of the fore arm, the radius being much more slender and crossing over the ulna from the outer to the inner side. (See Pl. XXII.)

Specializations

Size.—The grandeur of the elephant is a familiar thing in these days of zoölogical gardens and circus caravans, but rarely does one see a really huge specimen. The tallest living elephants belong to the African species, as those of India are longer and lower. "Jumbo" (Pl. XXI), the huge African elephant purchased by P. T. Barnum from the London Zoo, had a height of 11 feet and a weight of $6\frac{1}{2}$ tons! His weight but not his stature was exceeded by a huge Indian elephant in Barnum's herd some years ago. Wild African elephants are said to attain a height of 13 feet, while the largest American proboscidean was the imperial elephant of the early Pleistocene, whose stature equalled if it did not surpass

that of the African form. The greatest height recorded so far is that announced in the English press for a straight-tusked elephant, *Elephas antiquus*, discovered near Chatham, England, in a Pleistocene river terrace in the grounds of the Royal School of Military Engineering at Upnor. This 15-foot creature, now mounted in the British Museum, exceeds in size the great skeleton of *Elephas meridionalis* in the Paris Museum, which measures about 14 feet in height at the shoulder.

Pillar-like Limbs.—While the bones of the limbs and feet are primitive in their numbers and arrangement, they are modified in one way in that they lack the angulation characteristic of ordinary ungulates and are perpendicular one above another. Thus in the horse the thigh is permanently flexed at the knee so that its long diameter is always oblique, but that of the elephant is vertical. This produces an alteration in the shape of the bone itself, for in the horse it is an elongated S with the articular faces more or less parallel with the axis; in the elephant it is I-shaped, the articulations lying at right angles with the axis of the bone. As the stress is thus transmitted through the length of the bone, the latter may be flattened without serious detriment to its strength, which is impossible when the stress passes obliquely through the bone. We find this same type of limb again and again, as in the amblypod *Dinoceras* and the sauropod dinosaurs, and, while these creatures have not been observed in the flesh, the inference that their limbs were graviportal as an adjustment to weight-carrying is irresistible.

Shortening of the Neck.—As a rule, long limbs like those of the elephants are accompanied by a corresponding lengthening of the neck, as in the horse or more notably the giraffe, to enable the owner to reach the ground. This arrangement serves well enough where the head is comparatively small and there is no proboscis, but in the elephant the huge head could hardly be borne on a long neck, and besides, the proboscis obviates the necessity for this.

Proboscis.—The trunk of the elephant is in many ways its most distinctive feature and, indeed, gives the name to the order. It is the much elongated combined nose and upper lip, and the nostrils run the entire length, terminating at the tip, which is provided with one (Indian) or two (African) finger-like processes by which relatively minute objects may readily be picked up. The trunk is a great muscular mass with an enormous number of component muscles which by their coördinate movement shorten or lengthen

the organ as a whole or curl it about any larger object to be lifted. It abundantly compensates for the extremely short neck.

Form of the Skull.—Next to the proboscis, one of the most remarkable elephantine features is the peculiar proportions assumed by the skull, which has not only increased in actual size, but in height is all out of proportion to its length as compared with that of other animals. This is simply a mechanical adaptation to give leverage for the great weight of the trunk and its occasional bur-

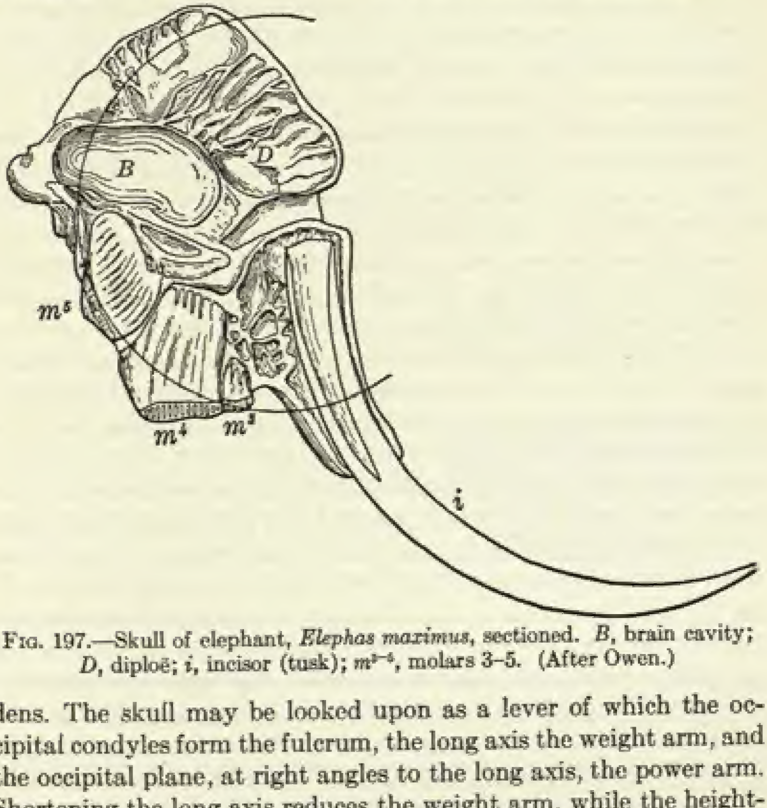


FIG. 197.—Skull of elephant, *Elephas maximus*, sectioned. *B*, brain cavity; *D*, diploë; *i*, incisor (tusk); m^{3-5}, molars 3–5. (After Owen.)

dens. The skull may be looked upon as a lever of which the occipital condyles form the fulcrum, the long axis the weight arm, and the occipital plane, at right angles to the long axis, the power arm. Shortening the long axis reduces the weight arm, while the heightening of the skull, especially at the occiput, lengthens relatively and actually the power arm, thus increasing the leverage and at the same time giving greater surface for the attachment of the great elastic ligament (ligamentum nuchæ) which runs backward to the vertebral spines and bears the weight of the head, and for the huge muscles of the neck. Thus not only is the power greatly

increased, but it is much more effectively applied through this "bulldogging" of the skull, as it has been called. The alterations in shape thus described do not carry with them an increase in the size of the brain cavity, but the outer and inner "tables" of the cranial bones have separated from each other and the intervening space has become filled with air-cells or sinuses separated by thin, apparently irregular, bony plates. To this cancellous bone with its air-cells the name diploë has been given. The sinuses are found in the skulls of other animals and of man where wide expansions of bone are developed, as in the skull of *Coryphodon* (page 512), but nowhere is the diploë developed to the extent found in the elephant.

Dentition.—Another highly characteristic proboscidean feature is the dentition, remarkable in three ways: fewness of the teeth present at any one time, tooth succession, and the development of the individual tooth itself.

An elephant (genus *Elephas*) never has normally more than one pair of tusks, which are the second upper incisor teeth, and one complete or two partial grinders in each half of each jaw, that is, 6 complete or 10 partially worn and partly formed teeth at any one time. Of course the total number of teeth is greater, 28 as compared with the normal 44, but instead of having a milk set, *succeeded* vertically by the permanent teeth, the teeth appear in numerical sequence. The upper milk tusks are succeeded by the permanent ones as in other mammals; the grinders, however, are formed one at a time in the rear part of the jaws and move downward and forward through the arc of a circle to replace those worn out by use. Owen tells us that the milk or deciduous tusk appears beyond the gum between the sixth and seventh month and rarely exceeds two inches in length and a third of an inch in diameter at its thickest part where it protrudes from the socket. The permanent tusk cuts the gum usually a month or two after the milk tusk is shed. The first molar tooth appears during the second week, is complete and in full use at three months, and is shed when the elephant is about two years old. The second molar has most of the plates (see page 464) in use at two years of age and is shed at six, the third appears at two, is at its maximum at five, and is shed at nine. These are looked upon as milk molars. The first true molar, which is the fourth grinder in succession, appears at the sixth year and is shed from twenty to twenty-five, the fifth shows its

crown at twenty and is shed probably at sixty, and the last molar appears at from forty to fifty years.

The tusks are spirally curved, elongated cones composed, except for a small patch of enamel at their unworn tip, entirely of dentine or ivory of superlative fineness. They are formed from a large conical pulp at the bottom of the alveolus or socket and grow continuously throughout the animal's life. Many other creatures, such as the rodents, have continually growing incisors, but with them the upper and lower teeth are antagonistic and are kept within limits by wear. With the elephant's tusks this is not true and while their use, especially that of digging, entails some wear, there is nothing to limit their monstrous growth. The tusks of the Indian or Asiatic elephant are comparatively moderate in size, the largest cited by Owen in his *Odontography* having a length of 9 feet with a basal diameter of 8 inches and a weight of 150 pounds; but, as he says, these dimensions are rare in the Asiatic species. The record for an African elephant, on the other hand, is that of a superb pair of tusks seen in New York, of which the right one was 10 feet $\frac{3}{4}$ inches long by 23 inches in circumference and weighed 224 pounds, while the left was 10 feet $3\frac{1}{2}$ inches long by $24\frac{1}{2}$ inches around and weighed 239 pounds, giving a total of 463 pounds for the pair! It is said that the creature that bore these tusks was so old and the tusks so burdensome that he occasionally had to stop and rest their tips on the ground. The females of both species usually have smaller and straighter tusks than the males, although the tusks may be vestigial in the Asiatic females and in the males as well. In certain of the extinct forms, notably the imperial elephant of southern United States and Mexico, the tusks are much larger, those of a specimen at Yale measuring more than 13 feet on the curve, while one in the City of Mexico is said to exceed 16 feet.

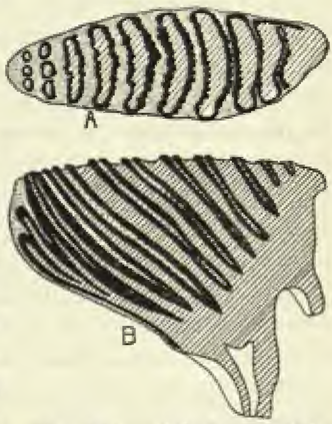


FIG. 198.—Molar tooth of elephant, *Elephas maximus*. A, crown view; B, sectioned longitudinally. Black, enamel; oblique lines, dentine; dots, cement. (After Lull.)

The molar teeth (see Fig. 198) are highly complex structures

made up of a number, up to twenty-seven or more, of transverse plates or lamellæ, each of which is composed of a flattened mass of dentine surrounded by enamel. The plates are united by a third substance known as cement so that as the crown wears away it bears a number of transverse ridges, formed of the harder enamel, separated by depressions at the bottom of which lies the softer cement or dentine as the case may be. The first teeth are relatively simple, but the number of plates and consequent ridges, two to a plate, increases with the size of the teeth until in the last molar the maximum of twenty-four for the Asiatic and ten or eleven for the African elephant is reached, the latter being more primitive in its tooth structure.

Brain.—As we have already seen, the brain is of an old-fashioned sort in that the fore-brain does not cover the hind-brain; on the other hand, its specializations lie in its great size[1], which actually twice exceeds that of man and is second only to the size of the brain of the great whales. In addition to its volume the elephant brain is noted for its convolutions but this is in part an adaptation to size, for the bulk of an object increases with the cube of its diameter, while the surface enlarges with the square; the one therefore outruns the other, and if they are to bear a definite ratio to each other the surface must be increased by infolding. Beddard speaks of the proboscidean brain as a great specialization of a low type.

The intelligence of the elephant has been exaggerated by some writers and greatly minimized by others. Elephants possess a remarkable memory of injuries, real or fancied; of misfortunes; of friend and foe; and of the time and place of the ripening of favorite fruits, as many a planter knows to his cost. They also learn to perform complex labors, such as the carrying and piling of logs in the teak yards of India without direction other than the initial order; they are obedient and docile, notably those of India, and this seems the more remarkable when it is remembered that they are not domestic animals in the sense of being the product of generations of selective breeding, but that practically every one is caught wild and subsequently tamed, so that these qualities of which we speak are inherent in the race.

[1] The brain of the fine male Indian elephant "Rya," recently presented by Ringling's Circus to the Yale Museum, weighed $10\frac{3}{4}$ pounds, the animal standing 8 feet 2 inches in height. This animal was tuskless.

But the docility, especially of the males, is subject to rude interruption by periods of nervous excitement, apparently of a sexual nature, known as "must," during which they become very dangerous and sometimes destroy the keepers in their paroxysms of rage. Ultimately all male elephants become surly and intractable; in the wild state such are known as rogues and live apart from their kind until they die. The great Asiatic elephant "Gunda" (see Pl. XXIII,B) in the New York Zoölogical Park, when purchased in 1904 was so docile that children rode upon his back. In 1908 he began to show signs of surliness and the following year made a murderous attack upon his keeper. In 1912 "Gunda" was put in chains for another savage assault, and in 1913 another keeper had a narrow escape from death. Finally in 1915 the beast had become so dangerous and so unhappy that in spite of being in every other way a superb specimen he was condemned to be destroyed. His age at the time of his death was about twenty-four years. The famous "Jumbo" was sold from the London Zoölogical Gardens because he was no longer trustworthy from the same cause. He was not, however, a confirmed rogue, even when he died three and a half years later. "Jumbo" was also twenty-four years old at the time of his death.

There is a certain parallelism between the nature of human mental development and that of the elephant. One of the most potent factors in the evolution of man's mind is his ability to handle various objects and thus bring them before the eyes for examination. This is also true of the elephant, although to a less extent, and undoubtedly has aided materially in its mental development.

Elephants have been accused of timidity and cowardice, though when brought to bay rage may simulate courage, making a charging tusker a most formidable foe.

Senses.—In common with most forest and jungle dwellers with whom opportunity for extended vision is rare, elephants are relatively dull of sight, though keen of scent and hearing, in fact, marvellously so, for Schillings, the German explorer, tells us that they either have an acuteness of some known sense far beyond our comprehension or some other sense unknown to us. The latter, however, is hardly possible and since the sentinels of the herd stand with uplifted trunk testing the breeze, it is probably in the sense of smell that elephants are thus gifted.

Evidences for Evolution

Ontogeny

But little is known of the earlier stages of elephant ontogeny owing to the great scarcity of embryonic material. The smallest and most immature embryo of which a description has been thus far published was pictured in *L'Illustration* for December 20, 1912 (see Fig. 199). In this picture the creature, whose length was but 17 centimeters (6$\frac{5}{8}$ inches), is seen astride an ordinary drinking glass (tumbler), but even at this early stage is essentially elephantine, proboscis and all. About the only thing noticeable in the picture wherein the specimen departs from the normal elephant is the marked angulation of the limbs and the relatively greater length of the foot below the heel. The embryo, which is that of an African elephant from the Congo, is also long-jawed, although this is not evident from the picture.

Fig. 199. — Embryonic elephant, *Loxodonta africana*, resting on a drinking glass. (Redrawn from *L'Illustration.*)

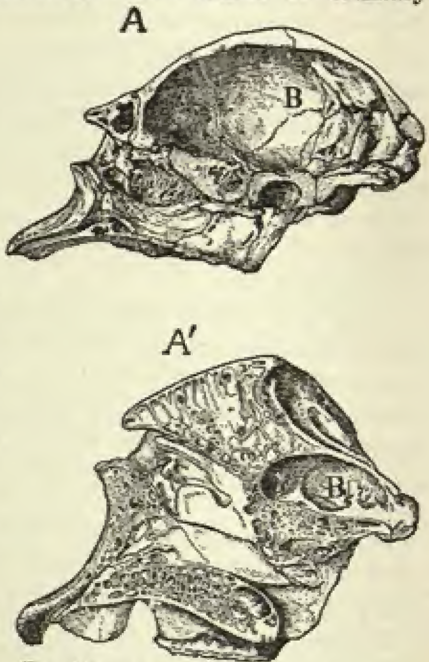


Fig. 200.—Sections of skull of (A) young and (A′) adult African elephant, *Loxodonta africana*, showing development of cellular structure or diploë with age. B, brain cavity. (After Flower.)

Aside from the gradual increase in tooth complexity with age, perhaps the most notable ontogenetic change is the heightening of the skull with the development of the diploë, for the cranium

of a new-born elephant is like that of other mammals, a comparatively thin-walled brain-case, the cavity of which increases but little in size with the growth of the skull as a whole, as the figure shows (Fig. 200).

Phylogeny

Size.—The phylogenetic changes, on the other hand, are amply recorded by the remarkably extensive series of fossil Proboscidea which have come to light. If *Mœritherium* (see page 572) is to be considered a proboscidean in the direct line of descent, its estimated height of three feet may be taken as the one extreme in the series, that of *Elephas antiquus* of fourteen feet as the other, an increase of about five diameters or 125 times in bulk.

Dentition.—The dental formula of *Mœritherium* may be expressed thus: incisors, $\frac{\text{upper rt. 3-lft. 3}}{\text{lower rt. 2-lft. 2}}$; canines, $\frac{1-1}{0-0}$; premolars, $\frac{3-3}{3-3}$; molars, $\frac{3-3}{3-3}=\frac{20}{16}=36$ teeth, a very slight reduction from the normal 44.

In *Phiomia* (see page 573) the formula is: i, $\frac{1-1}{1-1}$; c, $\frac{0-0}{0-0}$; p, $\frac{3-3}{3-3}$; m, $\frac{3-3}{3-3}=\frac{14}{14}=28$. In *Mastodon americanus:* deciduous teeth: i, $\frac{1-1}{1-1}$; c, $\frac{0-0}{0-0}$; m, $\frac{3-3}{3-3}=\frac{8}{8}=16$; permanent teeth: i $\frac{1-1}{0(1)-0(1)}$; c, $\frac{0-0}{0-0}$; p, $\frac{1-1}{1-1}$; m, $\frac{3-3}{3-3}=\frac{10}{8-10}=18$–$20$. *Elephas:* deciduous and permanent: i, $\frac{2-2}{0-0}$; m, $\frac{6-6}{6-6}=\frac{16}{12}=28$. Thus it will be seen that there is a gradual diminution in the number of the teeth during the progress of evolution; especially is this true with reference to the number present in the jaws at any one time.

In the earliest proboscidean (*Mœritherium*) the molar teeth are small and short-crowned, with two simple transverse crests and small hinder lobes separated by open valleys. As time goes on the number of cross crests becomes greater, although in the mastodons there are never more than five or six. The mastodons have, moreover, little or no cement in the intervening valleys, although the latter may be more or less interrupted by additional cusps. In some species the worn crests are comparatively simple, in others there is a more or less complex "trefoil" pattern of the enamel produced by wear.

The transitional elephants of the genus *Stegodon* (see page 579) have more complicated teeth, the crests increasing in number up to ten and becoming narrower; there is also a tendency toward the filling of the valleys with cement. In *Elephas* the deep-crowned

complex grinding teeth suitable for harsh herbage are perfected, reaching great intricacy in the woolly mammoth, *Mammonteus primigenius*, in which the number of crests may be twenty-five or more up to thirty. In the African elephant, *Loxodonta*, the teeth are less complex in that not only are the crests fewer, ten or twelve, but each becomes lozenge-shaped upon wear rather than having the form of a greatly compressed ellipse with parallel sides.

Tusks.—The earliest form, *Mœritherium*, has three incisor teeth above on each side, the second pair of which are larger than the others and point sharply downward; the second lower incisors are in the form of procumbent tusks almost horizontal in their position. *Phiomia*, the next stage, has a single pair of tusks above, with a broad enamel band, and a pair of spatulate ones below at the end of the elongating lower jaw. None of the tusks are continuously growing as in later forms. From *Phiomia* on, the tusks are borne in both jaws and grow continuously throughout life, the upper pair, which are curved downward, possessing an enamel band on their outer face. These are the four-tuskers or "tetrabelodonts." Subsequently most of the Proboscidea lose the lower tusks although vestiges, one or two, may be present in the male of the American mastodon. With the loss of the lower tusks the upper ones turn upward and finally lose their enamel, as in the form just mentioned and in the true elephants.

Lower Jaw.—The lower jaw also undergoes a remarkable evolutionary change, elongating at the symphysis with the development of the lower tusks until in the Trilophodonts a maximum is reached. In other phyla, with the loss of these tusks, it shortens until only a spout-like vestige of the old elongation remains. In the aberrant form *Dinotherium* the lower tusks are retained, but the jaw bends downward sharply at the symphysis so that the short, pointed tusks lie at right angles to the jaw. The upper tusks are apparently lacking. Tusks seem to have had for their stimulating function that of digging—first a spade-like use of the spatulate lower tusks, the upper ones having possibly a pickaxe-like function for loosening the earth. Later when the upper ones assume the entire digging function, as we have seen, they turn upward instead of down. The African elephant to this day is a most industrious digger and one tusk, as a consequence, is almost always the shorter of the two. The use to which *Dinotherium* put its lower tusks is conjectural; there is reason to believe, however, that it may have been partially

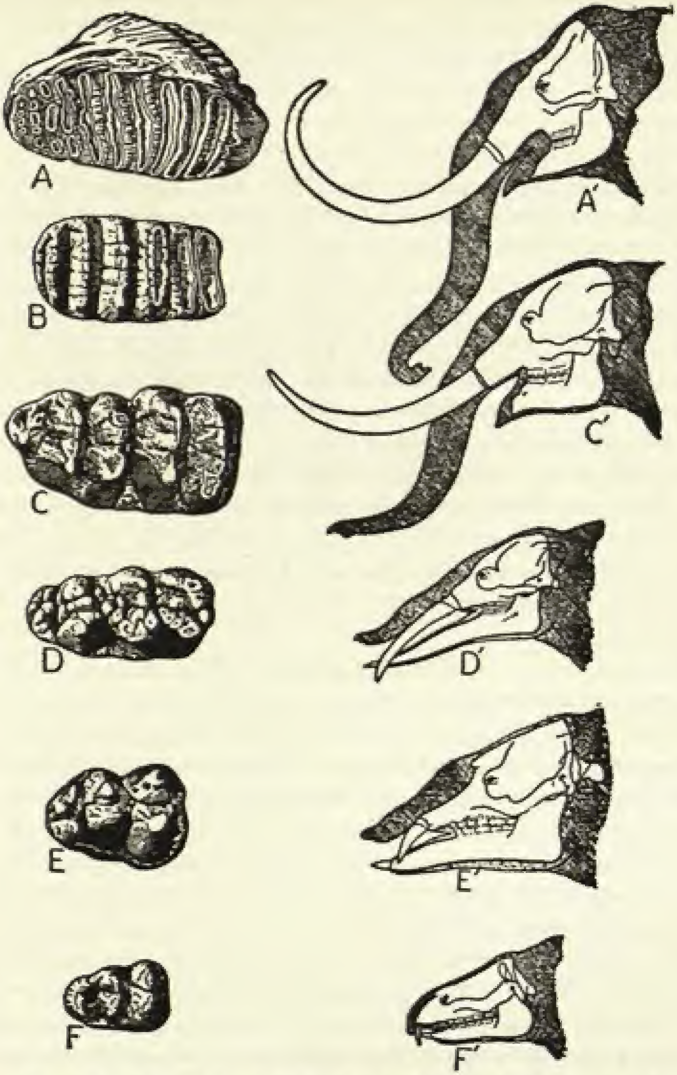


FIG. 201.—Evolution of head and molar teeth of mastodons and elephants. A, A′, *Elephas*, Pleistocene; B, *Stegodon*, Pliocene; C, C′, *Mastodon*, Pleistocene; D, D′, *Trilophodon*, Miocene; E, E′, *Phiomia*, Oligocene; F, F′, *Mœritherium*, Eocene. (After Lull.)

aquatic and the simplicity of its teeth points to a very succulent sort of food, possibly of aquatic or swamp vegetation; if so, the tusks may have been used for detaching it.

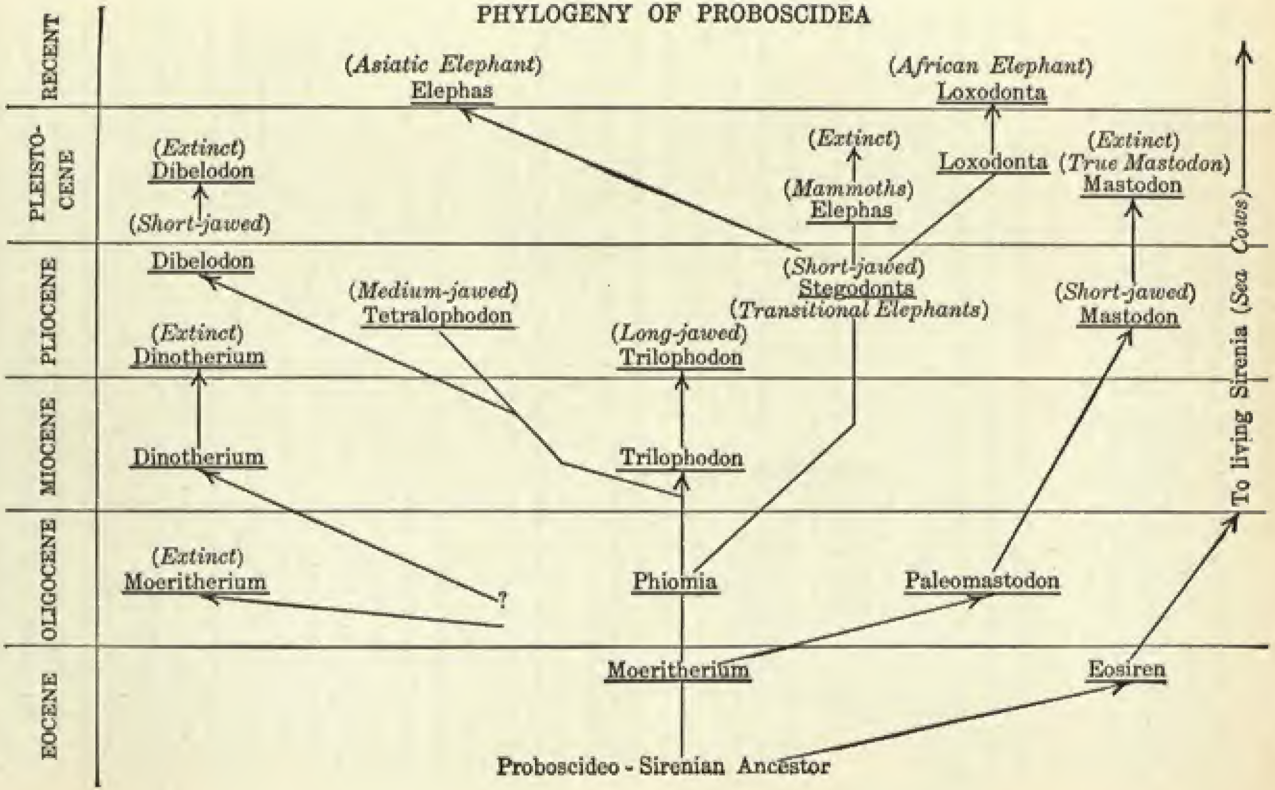
Proboscis.—The presence of a proboscis is always indicated by the shortening and backward retreat of the nasal bones, together with a strengthening of the adjoining bones for muscle attachment. There is therefore no reason to believe that *Mœritherium* bore a proboscis of any sort, although it may have possessed a prehensile upper lip; but even this cannot be proved. In *Phiomia*, on the other hand, the nasals have receded and the rear of the skull has begun to heighten, indicating that a proboscis had been developed probably merely for the purpose of reaching beyond the lower tusks. Thus the development of the latter seems to have been the prime cause of the growth of the trunk, which developed *pari passu* with the elongating lower jaw. Although the jaw was long, however, the proboscis was distinctly limited in its movement, for while it could be raised and swayed from side to side it could not be bent downward unless to one side of the jaw. The shortening of the jaw, or, as in *Dinotherium*, its downward curvature, left the proboscis as the wonderful pendent organ which the living elephant possesses.

Ancestry

Phylogeny.—As with the horses, the phylogeny of the Proboscidea is quite complex, and the final unravelling of it is not yet accomplished to the satisfaction of paleontologists. That set forth by C. W. Andrews in the *Guide to Elephants* in the British Museum (Natural History), while highly authoritative, is a simple story of successive stages, whereas the American paleontologist Osborn goes to the other extreme and recognizes many divergent and parallel races, no fewer than "twenty-eight generic and subgeneric phyla . . . with other phyla doubtless remaining to be discovered." This extreme differentiation has not yet been generally accepted. It is best, perhaps, to traverse a middle ground.

By Oligocene time the Proboscidea had branched into four principal stocks, the (1) Mœritheres, (2) Dinotheres, (3) Mastodonts, and (4) Elephants. Of these the swamp-dwelling mœritheres were doomed to speedy extinction. The dinotheres, while longer-lived, were few, a curious aberrant side line which died out in the Pleistocene. The mastodons, vastly more numerous and widespread, are differentiated into the true mastodons, with relatively simple

PHYLOGENY OF PROBOSCIDEA



teeth, which persisted until very late geologic time, and the bunomastodons, whose teeth were rendered more complex by the addition of cones and trefoils between the crests. They include long, medium, and short jawed forms, the last having lost the lower tusks, and were in general browsers. The last group (Elephantoidea) include the stegodonts or transitional browsing elephants and the true elephants which possess upper tusks only and very complex grazing teeth.

Early Tertiary Ancestors.—Our knowledge of the earlier stages is due largely to the work of C. W. Andrews, who had access to the vast amount of material in the British Museum of Natural History as well as that collected by the Egyptian Government and now preserved in the Cairo Museum. The Eocene and Oligocene stages, which are entirely African, are, first, the genus *Mœritherium* (Mœris, an ancient lake near which the remains were found, and θήρ, beast) (Figs. 201,F, F′; 202; 203), which comes from rocks of late Eocene and Lower Oligocene age in what is known as the Fayûm district of the Libyan desert, some sixty miles southwest of Cairo, Egypt.

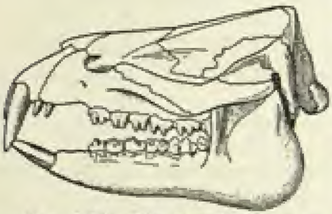


FIG. 202.—Skull of *Mœritherium lyonsi*, Eocene, Africa (Fayûm). One-tenth natural size. (After Andrews.)

The form is imperfectly known except for the skull, which is unlike that of any other proboscidean in that the face is short, the middle portion long, and there is no indication of a proboscis. However, it does show the beginnings of proboscidean evolution, since the nasal openings are large and are beginning to recede, the air-cells are beginning to form in the back of the skull, the second pair of upper incisors are enlarging into tusks, the molars are transversely ridged, and the anterior part of the lower jaw is elongating and becoming spout-like. So much of the skeleton as is known indicates an animal about three feet high. This creature was probably a swamp-dweller, living upon the succulent semi-aquatic herbage of the time. It is unrecorded

FIG. 203.—Head of *Mœritherium*, restored. (After Osborn.)

outside of the Fayûm, but seems to have existed into the Lower Oligocene so as to become a contemporary with the next genus.

The succeeding genus in the evolutionary series is *Phiomia* (Figs. 201E, E′; 204, 205) which was likewise discovered in the Lower Oligocene deposits near Lake Moeris in the Egyptian Fayûm but has more recently been reported from the Gaj horizon of northern India in the Siwalik hills. It is an undoubted proboscidean of larger size than its predecessor and with limbs much like those of modern types. The skull has increased materially in height, with a considerable development of diploë, and the small nasals with their openings have receded so that they lie just in front of the orbit much as in the modern tapirs. This would imply the development of a short extensile proboscis. The upper and lower canine and incisor teeth have entirely disappeared, with the exception of the second pair of incisors, which have become well developed tusks. Those of the upper jaw are large, downward curved, and have a band of enamel on their outer face. The lower jaw has elongated considerably, especially at the symphysis, and the tusks point directly forward as in *Mœritherium*. The premolar teeth have two and the molars three transverse crests composed of distinct tubercles while the hindermost tooth is tending to develop yet another crest. The neck is fairly long, although the posterior cervical vertebræ tend

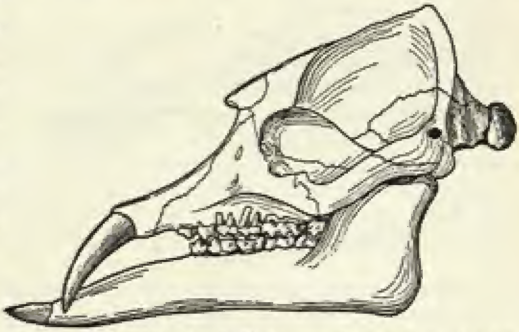


Fig. 204.—Skull of *Phiomia*, Oligocene, Africa (Fayûm). One-twelfth natural size. (After Andrews.)

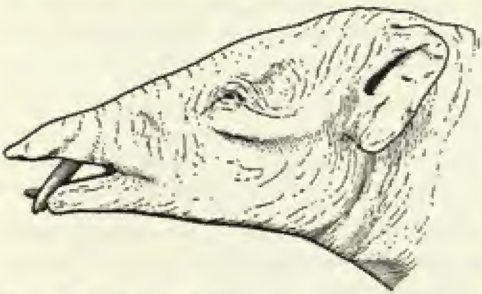


Fig. 205.—Head of *Phiomia*, restored. (From model by Lull.)

to shorten. The genus *Palæomastodon* is not well known,[1] certain species being removed to the new genus *Phiomia*. The former is looked upon as the direct ancestor of the true mastodons (*i. e.*, *Mastodon americanus*) from the simple character of its teeth, although the connecting series is lacking, probably because of forest-dwelling habits which do not make for ease of fossilization or subsequent discovery. *Phiomia*, on the other hand, although contemporary, has more complex molars and is believed to be the forerunner of the shovel tuskers.

FIG. 206.—Skull of *Dinotherium giganteum*, Lower Pliocene, Germany. One-fifteenth natural size. (From British Museum Guide to Elephants.)

Dinotherium (Gr. δεινός, terrible) (Figs. 206; 207), an extinct proboscidean whose remains have been found in the Miocene and Pliocene of Europe and India, differs remarkably from the contemporary mastodons, mainly in its dentition, in that the molar teeth, which are more numerous than in proboscideans in general and have the normal vertical succession, have but two transverse crests and a small hinder lobe. They are therefore the simplest of proboscidean molars. The upper tusks appear to be lacking, and, as we have seen, the lower jaw with its contained tusks bends abruptly downward at the symphysis. There is evidence for the presence of a well-developed trunk and the remainder of the skeleton is typically proboscidean. The oc-

FIG. 207.—Head of *Dinotherium*. (After W. K. Gregory, from Osborn.)

[1] Andrews, 1902.

cipital region of the skull slants sharply forward and contains no diploë, otherwise the skull and the body and limbs have much the proportions of the American mastodon. A gigantic skeleton from the Roumanian Pliocene, *Dinotherium gigantissimum*, is very long-limbed and exceeds the largest mastodon in stature. This species could hardly have been either semi-aquatic or swamp-dwelling, since both of these habitats imply short legs like the hippopotamus. We can, in fact, conjecture little of the origin or of the habits of the dinotheres, except that their food must have been of a very succulent sort. The line must have diverged from the main proboscidean stem very early, as even *Phiomia* is too far advanced to have given rise to it. It represents an aberrant side line of fairly long duration.

Later Tertiary Mastodons.—There is considerable confusion as to the precise relationship of the various species of later Tertiary mastodons and their exact phylogeny is not yet clearly understood, so the classification here given is tentative and subject to future revision.

It seems most natural to group together all of the four-tusked mastodons with the elongated lower jaw under the name *Tetrabelodon* (Gr. τετρα-, four, βέλος, dart, ὀδούς, tooth), but a study of their molar teeth seems to show that at least two parallel evolutionary lines would be thus included, both of which from the trend of proboscidean evolution passed through a four-tusked stage. Classifying them in this way we recognize two principal genera, *Trilophodon* (Gr. τρι-, three, and λόφος, crest) and *Tetralophodon* (Gr. τετρα-, four, and λόφος, crest) in which the intermediate molars (milk molar 4, molars 1, 2) have three and four cross crests respectively.

Trilophodon (Figs. 201,D, D′; 208) is the third stage in proboscidean evolution, if we omit *Dinotherium*, and is well represented by the Miocene *Trilophodon angustidens* of which a splendid specimen from Gers, France, is preserved in the museum of the Jardin des Plantes at Paris (see Pl. XXII). It was an animal of considerable size, nearly as large as the Indian elephant, but differing from it in the enormously long lower jaw, which with its contained tusks had reached a mechanical limit of efficiency. The downward curved, enamel-banded upper tusks do not reach much beyond the limit of those of the lower jaw. The adult molars have attained such a size that but two can be contained in a jaw at any

one time. Correlated with the great length of the jaws is a marked increase in the diploë of the skull. *Trilophodon* was a great migrant,

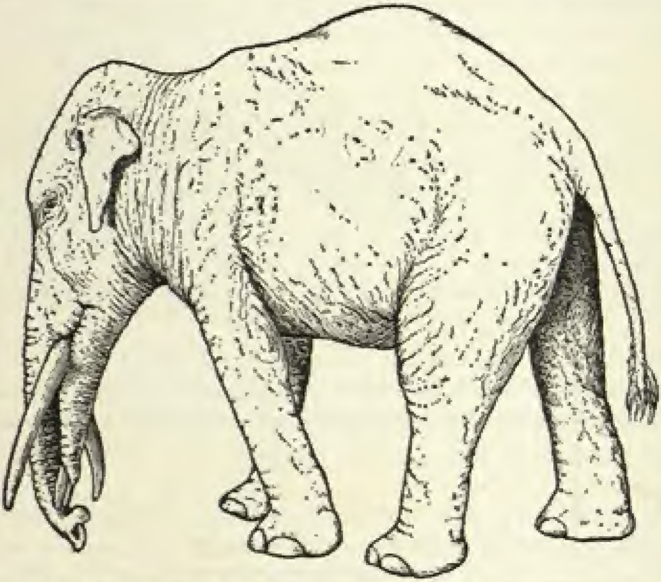


FIG. 208.—Restoration of *Trilophodon*. (From British Museum Guide to Elephants.)

for not only do we find its remains in Europe and Africa but it was the first proboscidean to reach North America and must have come by way of Asia early in Miocene time. Thereafter the Proboscidea formed an important element in the fauna of North America until the extinction of the American mastodon in post-Glacial time. *Trilophodon* (*Serridentinus*) *productus* is a well known Texas species from the Pliocene, while one American form, *Trilophodon lulli* (Fig. 209), from the Nebraska Pliocene, possesses a mandible at least 6 feet 7 inches in length, and the entire animal must have been ponderous. The

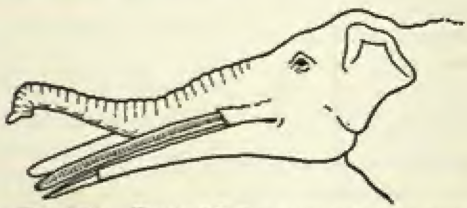


FIG. 209.—Head of *Trilophodon lulli*. The lower jaw, one of the longest recorded in any proboscidean, measured 6 feet 7 inches as restored. About 1/40 natural size. (After Barbour, from Kunz.)

type specimen, that of a very old animal, has but one badly worn molar left in each jaw. These are the Longirostrines of Osborn's classification.

In the genus *Tetralophodon* the jaws are not so elongated or so effective as digging organs, but this is compensated for by the greater complexity of the grinding teeth. Tetralophodonts are first known from the Miocene of Italy, but they reached India and finally North America, where they flourished and may have given rise to the peculiar South American mastodons known as *Dibelodon*, etc. (Osborn's Notorostrines).

In *Dibelodon* (Gr. δι-, two, βέλος, dart) (see Fig. 210) the molar teeth are similar and, because the intervening valleys are blocked by additional cusps, form, when worn, a rather intricate enamel pattern. It differs from the tetralophodont group, however, in

FIG. 210.—Skull of *Dibelodon andium*, Pleistocene, South America. (Modified from Burmeister.)

the loss of its lower tusks and the consequent shortening of the jaw. The enamel band of the upper tusks also tends to disappear and in its final stage we have a form not unlike *Mastodon* itself except for the greater complication of its grinders. *Dibelodon* is found widespread in the Pliocene of North America and, as far as we know, was almost the only proboscidean to reach South America, where it spread, one species along the Andean highland, another in the lower country to the east. They persisted into the Pleistocene in the southern hemisphere, but in the north were replaced by the true mastodon. There are also other curious American types known as Rhynchorostrines (beak-jawed) and Brevirostrines (short-jawed), which Osborn considers separate phyla.

The true mastodon, *Mastodon* (Gr. μαστός, breast, and ὀδούς, tooth) (Figs. 201,C, C′; 211; 212), is the best known of American proboscideans. The molars lack the intervening cusps of *Tetraloph-*

odon, so that the tooth is simpler in its appearance. The lower jaw is shortened in common with that of all later proboscideans, but as we have seen, vestigial and apparently functionless tusks may be present in some lower jaws, presumably those of males. The huge specimen, the so-called Warren mastodon, in the American Museum of Natural History, has one such tusk, while the Otisville specimen, a splendid young male mounted in the Yale Museum, has none, nor is there any trace of a socket. The mastodon attained a height about equal to that of the Indian elephant, from 7 to 9 feet, but was much stockier and more robust in build, a feature especially noticeable in the breadth of the pelvis and the massiveness of the limb bones. The skull also differs from that of the true elephants in its lower, more primitive contour, and although

FIG. 211.—Skull of *Mastodon americanus*, Pleistocene, North America. (After Lull.)

there is a large development of air-cells in the cranial walls, the brain cavity is relatively larger. The upper tusks are comparable to those of the elephants in the absence of enamel. Their length may exceed 9 feet. There are but two fully formed molars in the jaws at any one time.

The true mastodons were Pliocene and Pleistocene in range, outliving the elephants in North America. In geographical distribution they ranged from Europe across Asia to Alaska and thence southward throughout the United States. They seem to have been more exclusively forest-dwelling forms than the elephants which were their contemporaries. Their remains have been found chiefly as a result of drainage excavations in the swamps and boggy lands where they were doubtless mired and thus preserved from decay. This is especially true in New York, Indiana, Ohio, Illinois, Michigan, and Iowa, where it is said that almost

every bog contains a mastodon. The food consisted of twigs of hemlock, spruce and other evergreen trees, possibly other herbaceous vegetation as well, and one specimen found in Ulster County, New York, had preserved with the bones a quantity of long, dense, shaggy hair of a dark golden brown color.

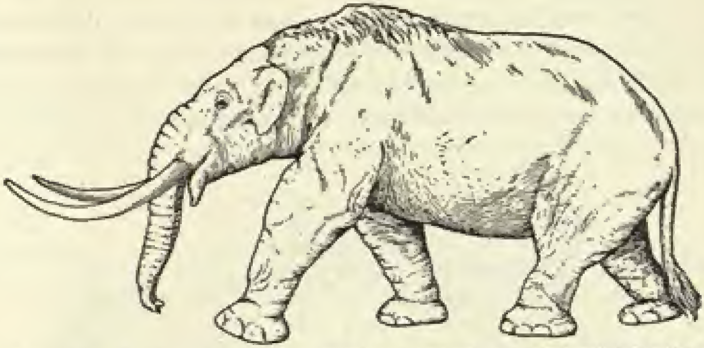


FIG. 212.—Restoration of the American mastodon. (After Knight, from Osborn.)

True Elephants.—In order to trace the evolution of the true elephants one must go back to the Upper Miocene of southern India, to the form known as *Stegomastodon latidens*. This creature gave rise to a species variously known as *Mastodon elephantoides* (*i. e.* elephant-like) or *Stegodon* (Gr. στέγειν, to cover) *clifti*, for its transitional character is such that authorities differed as to whether it is a mastodon or an elephant.

In *Stegodon* the molar teeth (see Fig. 201,B), have more numerous ridges than in the mastodons and the name is given because of the roof-like character of these ridges, the summits of which are subdivided into five or six small, rounded prominences. There is a thin layer of cement over the enamel in an unworn tooth, but no great accumulation of it in the valleys, in contrast with the elephants. These teeth show how slight the transition is, however; add merely a filling of cement to bind the crests together and the elephant tooth is formed. True *Stegodon* remains have been found only in southern and southeastern Asia, which suggests that that region may have been the original home of the true elephants.

The elephants have been sufficiently defined in the anatomical section of this chapter. Aside from the living forms, many species are found in the European Pliocene and Pleistocene and

two in North America, while another, the woolly mammoth, *Mammonteus primigenius*, is common to both and to northern Asia as well. The European species were *Elephas antiquus*, the straight-tusked elephant, and *Elephas meridionalis*, the former being the more primitive and showing the closest affinity with the living African species *Loxodonta*. Both these and *E. primigenius* were contemporaries of early man in Europe during the Glacial period. The American species are, first, *E. imperator* (Fig. 213), the larger, so-called imperial or southern mammoth, as its remains are found in Mexico, whence it ranged into Texas,

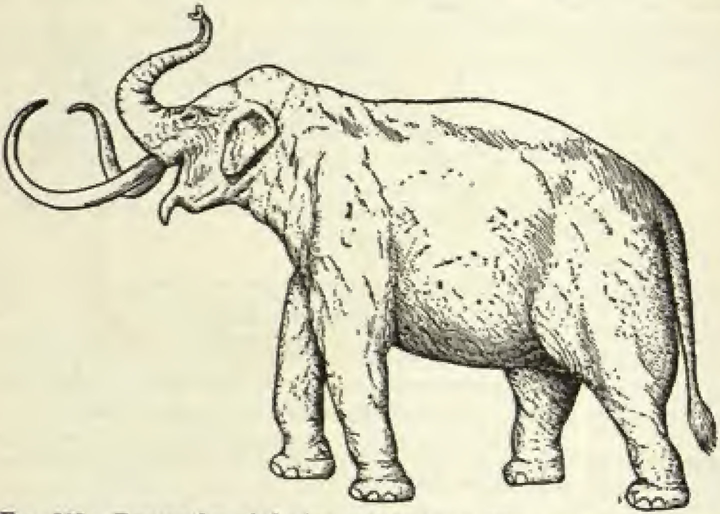


FIG. 213.—Restoration of the imperial elephant, *Elephas imperator*, Lower Pleistocene, North America. (Modified from Osborn.)

California, and as far north as Nebraska. A single molar tooth described from French Guiana seems to pertain to this elephant; if so, it is the only other species of proboscidean, aside from the genus *Dibelodon*, recorded from the southern continent. The molars of the imperial elephant are distinctive in that the crests are relatively few and the surrounding cement very thick.

The second American species is *Elephas jeffersoni*, the Jefferson elephant, a successor of *imperator*, distinguished by its lesser stature and more numerous crests to the teeth. Each of the American species seems to have been characterized by the extreme spiral form of the tusks which in old age actually crossed at the tip so

that their primal function of digging was utterly lost, nor were they efficient weapons of offense or defense. They have been cited as instances of evolutionary momentum, if such a thing exists, and certainly, so far as we can see, were detrimental to their owner rather than otherwise. *E. jeffersoni* is wide-spread throughout the United States up to the limits of the range of *M. primigenius*, which replaced it in the north. The distinction between the two species, however, is not always clear and there may have been transitional forms.

Mammonteus primigenius is the hairy or woolly mammoth, *the* mammoth of popular knowledge. It was admirably adapted

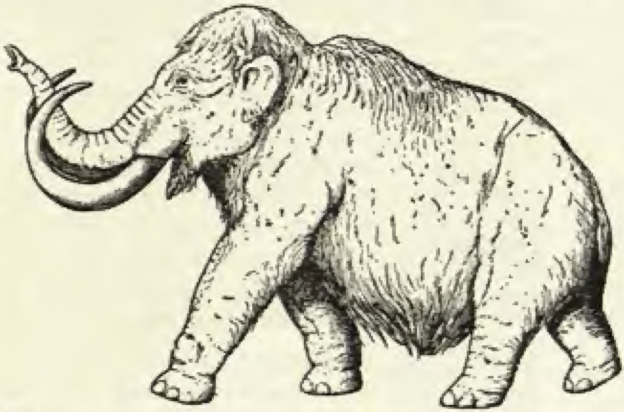


FIG. 214.—Restoration of the woolly mammoth, *Mammonteus primigenius*, Pleistocene, Eurasia and North America. (After Knight.)

to withstand the cold of the Arctic climate. This adaptation lay in the development of a coat of coarse, long, black hair with a thick coat of brown wool beneath. It was circumpolar in its range, being found in great abundance along the shores of the Arctic Ocean but extending southward into Spain and Italy in Europe and as far as North Carolina and California in the New World. The famous frozen specimens of the Siberian tundras, that of the Lena delta found in 1799, and that of Beresovka in 1901 now mounted in the Leningrad Museum, have been described in Chapter XXV. According to Matthew, the contents of the stomach show that these animals fed upon the same vegetation, grasses and sedges, birches, alders, poplars, etc., that prevails to-day in the far north. They must have been very numerous,

as their tusks constituted one-half of the commercial ivory annually available and represent thus far a herd of no fewer than 40,000 individuals—not of course those living at any one time, but the accumulation of centuries.

That the mammoth was a familiar animal to prehistoric man is attested by the numerous drawings of them made by the artists of the Upper Paleolithic age on the walls of caverns. The teeth of the mammoth reached a maximum degree of complexity, doubtless an adaptation to the harsh vegetation of the north. Their tusks were of two sorts, one shorter and straighter, the other a long spiral rivalling the tusks of the Jefferson elephant. In size the mammoth, despite its name, was not great, as it rarely if ever exceeded the stature of the Indian elephant of to-day.

Living Elephants.—There are but two well-defined species of elephants extant and these are reaching the natural limits of their racial life. They are, first, the Indian or Asiatic elephant, *Elephas maximus* (Pl. XXIII,B) which inhabits the forest regions of southwest and northwest India, Ceylon, Burma, Assam, Siam, Cochin China, Sumatra, and Borneo. During the hot season they are confined to the denser parts of the forest, generally near water, while during the rainy season they range into the open, feeding on the tender grasses.

Fig. 215.—Molar tooth patterns of (A) African elephant, *Loxodonta africana*, and (B) Asiatic elephant, *Elephas maximus*. (From British Museum Guide to Elephants.)

The Indian elephant differs from the mammoths in the possession of five hind toes to four in the latter and in never having the huge spiral tusks; indeed, as we have seen, their tusks seem to be disappearing, even in the males. Their ancestry is unknown, as they could not have been derived from any discovered mammoth. The grinding teeth, however, are very similar to those of *Elephas jeffersoni*.

The African elephant, *Loxodonta* (Gr. λοξός, slanting) *africana* (Pl. XXIII,A) is distinguished by its greater size, enormous ears, lower forehead, and larger tusks, also by the character of its grind-

ing teeth (see Fig. 215). It is confined to the wooded districts of Africa south of the Sahara and north of the Cunene and Zambesi rivers, but in many districts it is becoming extremely scarce, largely owing to the persecution of the ivory hunters, for its ivory is of a finer quality as well as being more abundant than that of the Indian species. It is probable that in the course of a few years not a single *old* individual will be left alive, and unless they are protected by law they are doomed to a speedy extinction. The African elephant is rarely tamed, although it may be fully as tractable as its relative. A number of subspecies of African elephants have been described, most of which are geographical races differing mainly in the form and proportions of their ears. (See also "Jumbo," Pl. XXI.)

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CHAPTER XXXVI

HORSES

The evolution of the horse has for humanity a very deep interest because of the debt of gratitude which man owes to this humble servitor and comrade and because of the fact that, largely through the unwearying efforts of Professor Marsh of Yale University, a collection of fossil horses was there assembled which was to prove one of the first documentary records of the evolution of a race.

The American Museum of Natural History under Osborn's direction has since assembled an immense amount of material which gives a very clear view of the evolution of the group; it proves, however, to be not the simple sequence of genera of the earlier authorities but includes a number of diverging lines or phyla, the interrelationships of which are not yet fully understood. Loomis of Amherst College has also secured an interesting series of forms, including several complete skeletons, and more have been added to the Yale collection since Marsh's time.

Equine Adaptations

The adaptations undergone by the horse are in their last analysis reducible to two things, the perfection of the mechanism for food-getting and of that for speed, which constitutes the principal means of defense; and the influence upon the creature of these two groups of modifications is so great that the entire body shows specialization and we cannot, as in the elephants or in the human body, point to a number of primitive characteristics with a veneer of specialization along certain narrow lines. Hence we may dismiss the consideration of archaic features in the horse and pass at once to its specializations.

Body Contour.—Many of the equine adaptations have been referred to in Chapter XIX; it is only necessary to summarize them with exclusive reference to the horse. In order to reduce air resistance the body, neck, and head are smoothly rounded, with no needless excrescences and with perfect symmetry of form, so that a running horse with head extended and ears laid back con-

forms to the "numerical" or stream-lines almost as perfectly as does a bird or even a fish. This same symmetry is seen in the limbs, long and slender distally, and with the powerful muscles bunched at shoulder and thigh where they blend more or less with the contour of the body, the force being transmitted to the feet by long slender tendons. This concentration of the weight high on the legs, as we have seen, quickens their rate of movement without diminishing the length of stride.

Limbs and Feet.—The limbs themselves have departed widely from the ancient plantigrade gait of their primal ancestry and are unguligrade in that only the tip of the single toe, encased in its modified nail, is in contact with the ground; the wrist, the so-called fore knee, and the ankle, or hock, being raised high above the medium of support. Thus the lengthening of the distal limb segments is obtained not only by the actual elongation of the bones themselves but also by their posture. The reduction of digits is extreme, the horse being one of the few mammals which ever attained monodactyly, although the equivalent reduction in the artiodactyl or even-toed foot to the irreducible minimum of two has been reached several times.

This diminution of digits carries with it a corresponding reduction of the second bone of the lower segment of each limb, that is, the ulna of the fore arm and the fibula of the lower leg. In the former case, especially, this means a restriction of motion, for it is only by the combined action of both radius and ulna that the rotary movement of the hand upon the arm is effected. Only the proximal third of the ulna, which forms the great portion of the elbow joint, is retained. All of the limb joints with the exception of the hip and shoulder are of the tongue and groove variety, their motion being thereby limited to the fore-and-aft plane. Within the limits thus imposed, however, the range of movement is very great. The shoulder girdle is reduced, as in all cursorial types, in that the clavicle or collar-bone has disappeared and there is no bony connection left between the shoulder blade and the remainder of the skeleton. This also permits great freedom of motion in the limited plane.

Lengthening of limbs implies a coördinate elongation of the neck and skull in contrast with the lack of such modification in the elephant. In general there is in a cursorial form a recognizable "speed index," as indicated by the ratio of length to diameter in

the limb bones; and not only does this ratio hold for each of the several bones concerned in locomotion, but it may also be seen in the skull, vertebræ, ribs, and other skeletal elements as well. The hoof which terminates the single remaining digit is a marvel of perfection; strong, of the right rate of growth to offset a normal wear, and with the shock-absorbing cushion or frog to guard the system from the great concussion produced by the impact of the foot with the ground at high speed. The perfection of the foot and limb to withstand such a shock is illustrated by the jumper "Heatherbloom," a horse which held a record of 8 feet 2 inches, in which the entire weight of the animal, coming from such a height, was repeatedly received on what is equivalent to the middle finger of the two hands. That the limit of such evolution has practically been reached, however, is evident from the fact that many a fine horse has been destroyed merely because a rutted road caused the fracture of a single bone strained beyond endurance. Bone is a wonderfully efficient material and it is utilized in what is mechanically the very best possible way to produce results, but with a very close margin of safety. It is this last fact that makes further speed adaptation for so large an animal virtually impossible.

Skull.—The skull is characterized by a large and well-developed brain-case, orbits completely surrounded by bone, and an elongated face, the purpose of which is twofold, first the raising of the eyes as far above the ground as possible while grazing in order to increase the range of vision, so essential for safety's sake, and second to allow room for the development of the deep-crowned grinding teeth. The elongation of the jaws separates without reduction in their numbers those teeth which are concerned with the prehension of food—the incisors—from those whose function is that of mastication—the premolars and molars. Incidentally the gap or diastema thus produced forms a convenient place for the bit and thus aids in the subjugation of the creature by man, but this was hardly nature's purpose.

Teeth.—There is a tendency toward tooth reduction for the first premolar, the so-called "wolf tooth," which is small and simple, is rarely present and soon shed. Then, too, the tusks or canines are rarely developed in the female, the upper ones never, although the normal male always possesses both. Sex characters are so rarely distinguishable among fossil forms that the lower jaw of a Miocene horse (*Merychippus*) in the Yale collection, in which

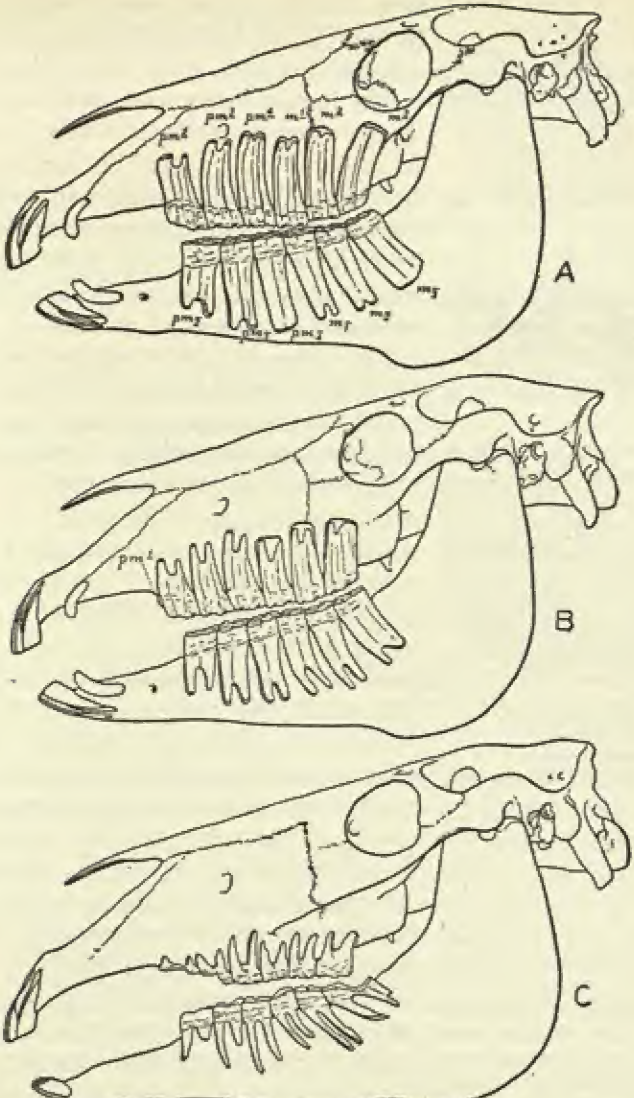


Fig. 216.—Dental battery of adult horse. A, five years old, permanent teeth all in use. B, eight years old, crowns reduced in length by wear and roots grow longer; vestigial first upper premolar ("wolf tooth") present. C, thirty-nine years old, lower molars incline forward, canines absent (female). pm^{1-4}, premolars 1–4; m^{1-3}, molars 1–3. (After Chubb.)

there is absolutely no trace of canines, was at once hailed by its discoverer as that of a mare.

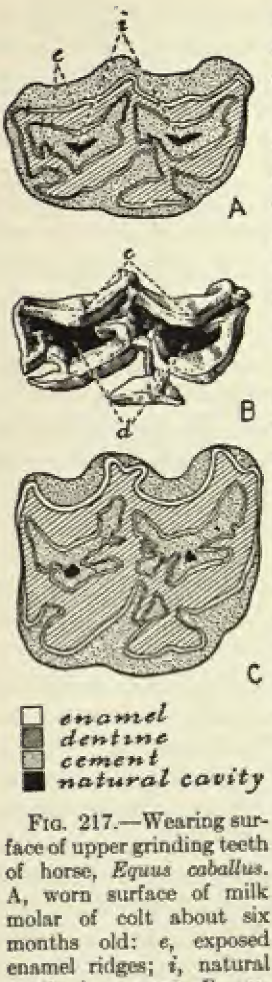


Fig. 217.—Wearing surface of upper grinding teeth of horse, *Equus caballus*. A, worn surface of milk molar of colt about six months old: *e*, exposed enamel ridges; *i*, natural cavity in cement. B, unworn surface of milk molar of colt three months before birth: *d*, cul-de-sac to be filled later with cement; *e*, enamel. C, premolar of horse eight or nine years old. Natural size. (After Chubb.)

The incisors or cropping teeth are long-crowned and are, with the single exception of *Macrauchenia*, a peculiar ungulate of the South American Pleistocene, unique in possessing a pitlike depression or "mark" in the grinding face. This mark, which is worn away with use, is one of the best criteria of its possessor's age.

The three molars and three preceding premolars of each jaw have become deep-crowned (hypsodont) grinding teeth, having the form of slightly curved prisms strengthened by three buttresses on their outer, convex face. The teeth are composed of the three materials which characterize the elephant's tooth—dentine, enamel, and cement—elaborately interwoven when seen in cross-section. As these substances differ markedly in hardness, differential wear produces a characteristic "pattern" of the more resistant enamel upon the wearing surface. For a while the teeth continue to grow, extending deeper and deeper into the jaw and at the same time moving slowly outward to compensate for wear. Finally, at about five to eight years of age, the dimensional limit of the jaw is practically reached, which of course makes further growth of the tooth impossible. Then the roots are formed and the tooth is completed. The outward movement, however, still continues, cancellous bony tissue filling the gradually vacated socket until the tooth is so nearly consumed as to be of no further service, when it is shed. The rate of growth and the outward movement are in absolute accord with the normal rate of wear, and the entire

tooth length is such as to last throughout the potential lifetime of the animal, about 34 years. With its final consumption malnutrition results, which, coupled with other evidences of senility, summons the horse to its final rest (see Figs. 216 and 217).

Size.—Another equine characteristic is size, for aside from the elephants, rhinoceroses, and hippopotamuses, the horse compares favorably with any terrestrial animal, being equalled only by the larger bovines, the cattle, buffalo, and bison. This is of course especially true of certain domestic strains such as the Percheron horses, some of which reach a shoulder height of 19 hands or 76 inches and a weight of over 2,400 pounds. On the other hand, the Shetland ponies are reduced in size, largely due to the harsh, restricted conditions of their island home, but aided by selective breeding. The following comparative measurements are given by Chubb for two animals the skeletons of which he has most admirably mounted in the American Museum of Natural History:

	Giant Draft Horse	*Shetland Pony*
Height at shoulders	6 ft. 1 in. (18¼ hands)	2 ft. 9⅝ in. (8½ hands)
Weight in life	2370 lbs.	170 lbs.
Bulk of humerus	118¾ cu. in.	9½ cu. in.
Bulk of femur	188 cu. in.	13½ cu. in.

Brain and Mentality.—The brain is not only of considerable size but is of a relatively high type compared with those of other mammals, and is richly convoluted. The intelligence of the horse is great but not equal to that of the elephant. As compared with the cattle, on the other hand, the horse is much more intelligent and is able to keep out of trouble and care for itself under trying conditions which may prove fatal to the former. The docility of the horse and its ability to learn not only from its master but also from experience are notable. On the other hand, it is emotional and its psychology is largely linked up with its normal mode of defense—flight—for the first impulse of a domestic horse upon seeing any incomprehensible thing is to run away, sometimes to its own and its owner's destruction. In the wild state this same impulse in an unarmed animal is of the greatest possible value as a means of survival.

Senses.—All three of the major senses, sight, hearing, and smell, are well developed; of the three, hearing is perhaps of the least importance to a plains-dwelling creature, just as sight is to one which is forest bred.

Evolutionary Summary.—Briefly stated, the evolutionary changes which the anatomy of the horse would lead us to predict are:

Increase in size.

Lengthening of the limbs.

Reduction of ulna and fibula, with a consequent limitation of the range of movement.

Change of foot posture from semi-plantigrade to unguligrade.

Reduction and loss of digits from five to one.

Perfection of the hoof.

Perfection of the dental battery in elongation and complexity of teeth.

Premolars becoming successively molariform.

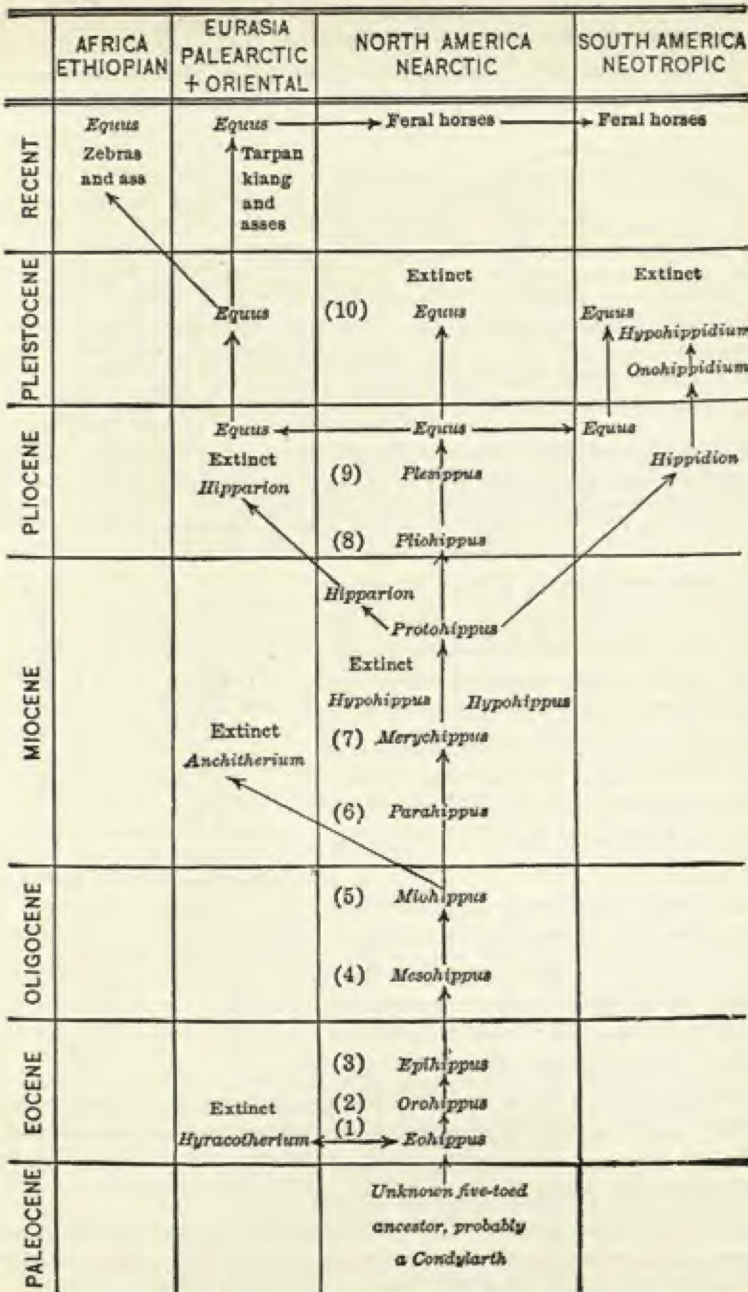
That these changes are all recorded in the paleontological record is conclusive proof of equine evolution.

Paleontology of the Horse

Place of Origin.—We have spoken of the simultaneous appearance of the modernized mammals in the Old and New Worlds, and the consequent belief in their origin in some contiguous land-mass which has been called boreal Holarctica. What is true of the modernized mammals in general is true of the horses in particular, although as yet it is incapable of actual demonstration. The London Clay, however, an Eocene formation of Europe, has produced *Hyracotherium*, the Old World's most ancient known equine, while in the Wasatch rocks of western North America, of nearly equivalent age, the earliest American genus, *Eohippus*, has been found. These two genera are very much alike, but the premolar teeth of *Hyracotherium*, especially the second one of the upper jaw, are more simple than in *Eohippus*, thus stamping the Old World type as the most primitive horse-like form known.

Horses are found from time to time in Europe and Asia as one ascends the geologic column, but the sequence does not seem to be continuous as it is in North America. Hence the inference that North America was the real theater of equine evolution, while the Old World horses were merely the relics of genera which migrated thence from time to time as barriers to dispersal were temporarily removed. The earlier of these migrations, while interesting, are unimportant from the standpoint of the evolutionary continuity; had it not been, however, for the final Pliocene migra-

PHYLOGENY OF THE HORSES



tion of the horses to the Asiatic and African continents within whose fastnesses they found asylum, their inexplicable extinction in the New World during the Pleistocene would have closed the book of their progress forever, and we would see them only as our paleontologic vision is able to pierce the gloomy curtain of the geologic past.

Fig. 218.—Restoration of four-toed horse, *Eohippus*, Lower Eocene, North America. (After Lull.)

Eocene.—Several generic names have been applied to the Eocene horses, of which *Eohippus*, the dawn horse, and *Orohippus*, the mountain horse, are the best known American forms. The first comes from the Lower Eocene (Wasatch) formation, and the latter succeeds it in the Middle Eocene Bridger beds. Both are from Wyoming and New Mexico.

The Eocene was a time of warm, moist climate, during which North America was clothed with a luxuriant vegetation, forests in which grew both evergreen and deciduous trees of a distinctly modern character, and, beside the numerous streams and lakes, sedgy meadows which in turn gave rise to grassy plains. Such was the environment of the first known horses which were already somewhat advanced toward their evolutionary goal.

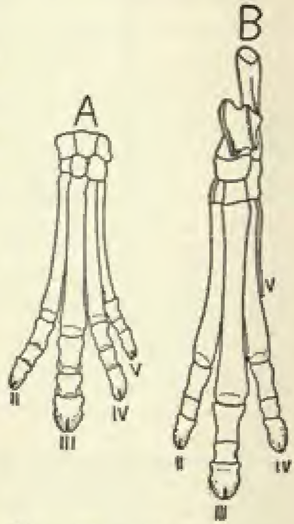


Fig. 219.—Hand (A) and foot (B) of *Eohippus*. One-half natural size. (After Marsh, from Lull.)

Eohippus, the four-toed horse (Figs. 218–220), represents the first recorded stage in equine evolution. It was a small but graceful creature, averaging about 12 inches or 3 hands in height at the withers, the several species ranging in size from that of a cat to a fox terrier, with arched back, short head and neck, limbs of moderate length, and showing in the digitigrade character of the feet the beginnings of cursorial adaptation. In fact, the general proportions are much those of a dog such as the fox terrier or the whippet. The hand bore four complete toes, each terminating in

a hoof-like nail, with no trace of the first digit or pollex, while the foot had but three, although vestigial remnants of the first and fifth are also seen. The advance of evolutionary progress shown by the foot over the hand is interesting, for it shows the foot to have been the main propelling organ and therefore the first to feel the influence of cursorial adaptation, and it also shows the reluctant relinquishment of general utility for mere propulsion on the part of the hand. Both ulna and fibula, while slender, are separate and complete. The modern tapir has feet in much the same stage of evolution as were those of *Eohippus.* The dentition is also advancing in that the molars already begin to foreshadow their future complication. The originally separate cusps are fusing into cross crests, and the fourth premolars are tending to become molariform.

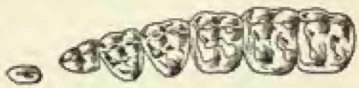


FIG. 220.—Upper teeth of *Eohippus.* Short-crowned, no cement, premolars simpler and smaller than molars. Natural size. (After Matthew.)

In *Orohippus,* the second stage (Fig. 221), a further advance is indicated by the loss of the splint of the fifth digit of the foot, the slight increase of size of the middle and the shortening of the outer finger of the hand, and the further perfection of the molar-like character of the third and fourth premolars. *Epihippus,* from the Upper Eocene Uinta formation, goes yet further in that the third and fourth premolars are completely molariform. The digits of the hand are still four, the outermost has diminished yet more but is still functional; the digits of the foot are three, but the middle digit of each begins to be the dominant one. There is on the part of the Eocene horses a gradual increase in size, the type skeleton of *Orohippus* mounted at Yale measuring $13\frac{1}{2}$ inches in height; *Epihippus,* the third stage, was still larger, but the complete skeleton is as yet unknown. *Epihippus* may not be the direct ancestor of the known Oligocene horses to be described.

FIG. 221.—Restoration of four-toed horse, *Orohippus,* Middle Eocene, Wyoming. (After Lull.)

The known range of Eocene horses from Europe to New Mexico

speaks for their migratory powers, always a characteristic of the equine hordes.

Oligocene.—The Oligocene was a time of increased aridity due in large part to continental uplift, and while much the same conditions prevailed as in the Eocene, there was a consequent dwindling of streams and lakes which gave impetus to the development of broad meadow lands and of true prairie as well. Thus there were three conditions—woodland, meadows, and dry prairie—which seem to have given rise to several divergent lines of equine evolution, some of which terminated, being overcome in the struggle for existence, while others flourished and gave rise to the horses of the Miocene.

Fig. 222.—Restoration of three-toed horse, *Mesohippus*, Middle Oligocene, North America. (After Lull.)

But two genera of Oligocene horses are recognized, *Mesohippus* and *Miohippus*, the fourth and fifth stages, the former one Lower and Middle Oligocene, the latter confined to the Upper Oligocene. *Mesohippus* (Figs. 222–224), which had attained the size of a prairie wolf, had three functional digits in both hand and foot, although a very short splint bone represented the fifth digit in the former. The middle toe in each instance was much the largest and the lateral ones in consequence bore less of the creature's weight. The shafts of both ulna and fibula are still complete but are thin and slender. *Mesohippus bairdi*, the best known form, averaged about 18 inches or $4\frac{1}{2}$ hands in height and was a slender-limbed creature, very well adapted for speed. *Mesohippus intermedius* was larger, fully the size of a collie, averaging 24 inches

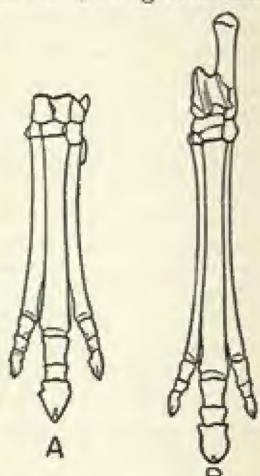


Fig. 223.—Hand (A) and foot (B) of *Mesohippus*. Over one-fourth natural size. (After Marsh.)

or 6 hands in height, and was in some ways unprogressive, which, together with the conditions under which it is found, may be

FIG. 224.—Upper teeth of *Mesohippus*. Short-crowned, no cement, second, third, and fourth premolars like molars. Natural size. (After Matthew.)

taken as indicative of a conservative forest-dwelling form in contrast with the progressive plains-living type. In all Oligocene horses the premolar teeth, with the exception of the small, simple, first premolar, are fully molariform. *Miohippus*, of the Upper Oligocene, is hard to distinguish from *Mesohippus*, except that the species average larger in size.

Miocene.—The Miocene was a time of great continental elevation and witnessed a wide expansion of our western prairies and a further diminution of the forest-clad areas. As a consequence, many browsing animals, well fitted for survival under former conditions, could not endure the change and perished, but the grazing types, horses, camels, deer, and antelope, adapting themselves to the new conditions, throve and spread amazingly and became the dominant forms of mammalian life.

The Miocene horses were several, representing at least three lines of adaptation, two of which, *Merychippus* and *Hipparion*, were to survive, while another, *Hypohippus*, was doomed to racial extinction.

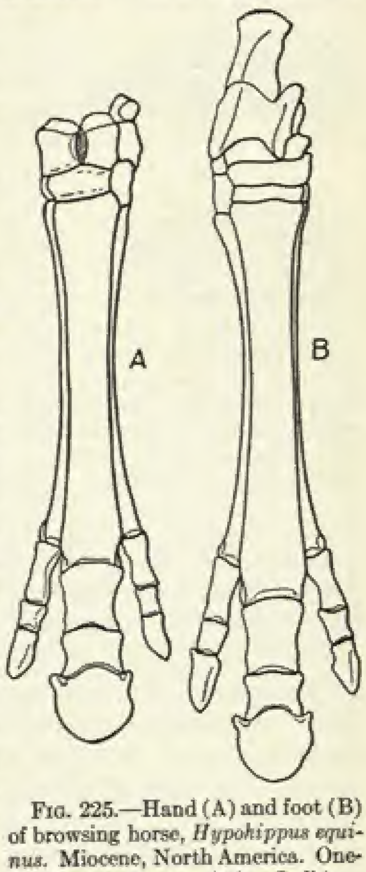


FIG. 225.—Hand (A) and foot (B) of browsing horse, *Hypohippus equinus*. Miocene, North America. One-fourth natural size. (After Lull.)

The Lower Miocene horse, *Parahippus*, represents the sixth stage, the older species being very much like *Miohippus*, while the later ones are almost indistinguishable from *Merychippus*. It is therefore fully transitional. In *Parahippus* for the first time the valleys between the crests of the teeth begin to fill up with cement formed as a deposit of "tartar" on the emerging portion of the crown. The amount of cement becomes progressively greater with the successive species. The lateral toes vary greatly; in some they are nearly as well developed as in *Miohippus*, in others much reduced.

Hypohippus (Fig. 225), known as the browsing horse, had broad, low-crowned teeth fitted only for browsing on succulent herbage. The feet were three-toed, which was equally true of all Miocene horses, but were distinctive in their broad spreading character, with well developed lateral hoofs as though adapted, like the living caribou, to a soft yielding ground rather than hard prairie soil. In the hand, vestiges of the first and fifth digits may yet be seen as small nodules of bone at the back of the wrist. Thus in spite of its having attained the size of a pony, 40 inches or so in height, the creature was otherwise persistently primitive and did not long continue to exist. A huge form, *Hypohippus matthewi*, lately described from the Nebraska Pliocene, greatly exceeded the more typical *Hypohippus equinus* in size.

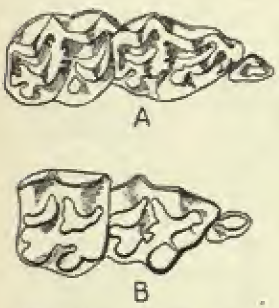


Fig. 226.—Upper premolar teeth of *Merychippus*, Upper Miocene, North America. A, uncemented milk teeth; B, cemented permanent teeth. (After Lull.)

Merychippus, the seventh stage in the direct line (Figs. 226, 227), appears in the Middle Miocene and is of especial interest in that it marks the transition from the horse-like forms with short-crowned, uncemented teeth (hyracotheres) to the true horses whose long-crowned, fully cemented grinders are suited to the harsh vegetation of the plains. In *Merychippus* the milk teeth are short-crowned and have little or no cement and are thus reminiscent of its ancestry, while the permanent teeth are intermediate in length of crown and quite heavily cemented and are thus prophetic of the future. This is one of the most remarkable instances of the ontogenetic evidence of evolution seen among the horses.

Merychippus is three-toed, in some instances with vestiges of the outermost digits of the hand. The lateral toes vary somewhat in the different species, though never reaching the ground, so that while structurally three-toed, the feet are functionally one-toed. The slender shaft of the ulna, which is free in the colt, is always fused with the back of the radius in the adult. The skull of this genus is the first in which the hinder border of the orbit is completed by sending downward a bony bar to join the zygomatic arch.

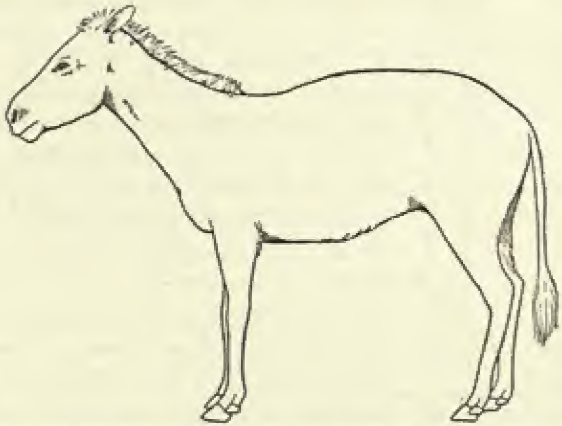


Fig. 227.—Restoration of the Miocene prairie horse, *Merychippus*. (After Lull.)

Protohippus and *Pliohippus* (Figs. 228, 229) of the Upper Miocene and Pliocene are two closely related genera, in fact the distinction between them is not always clear. It may suffice to say that *Protohippus* represents a form derived from *Merychippus* but differing in that the milk as well as the permanent teeth are moderately long-crowned and cemented, and in that the hand and foot still bear three toes; while in *Pliohippus*, the eighth stage, we have the first one-toed horse, although in some species the lateral toes seem to have persisted. *Pliohippus* is also characterized by having a peculiar pit or depression in front of the orbit which may have lodged a scent gland like the larmier of deer and possibly of similar function. The depressions also vary greatly in degree of development, so that they do not seem to have had an essential function. *Pliohippus* had a shoulder height of some 40 inches or 10 hands.

Yet another Miocene horse was *Hipparion* (Figs. 230, 231), closely related to the two preceding genera, from the former of which it is sometimes difficult to distinguish it. The following diagnostic characteristics are based upon a skeleton of *Hipparion whitneyi* from South Dakota, preserved in the American Museum. "This species, except for the very large head, had the graceful and slender proportions of the antelopes, but in *Protohippus* and especially in *Pliohippus* the skeleton approached more nearly the stockier proportions of the modern horses. The *Hipparion whitneyi* is regarded by Professor Osborn as fitted to live in a semi-desert country, and in contrast to the *Hypohippus*, is called the 'three-toed desert horse'" (Matthew). The argument for this belief is seen in the highly perfected teeth, the pattern of whose enamel is in some instances more complexly infolded than in any other horse, doubtless an adaptation to the harshest of herbage. The splendid fleetness which the skeleton implies is corroborative evidence.

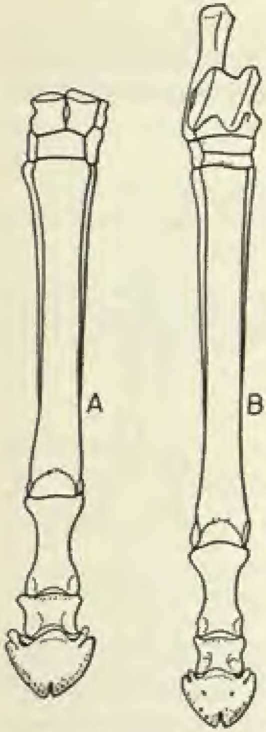


Fig. 228. — Hand (A) and foot (B) of the first one-toed horse, *Pliohippus pernix*, Pliocene, Nebraska. One-fourth natural size. (After Lull.)

Hipparion is another world migrant, as its remains are found not only in Colorado, Nebraska, and South Dakota in great abundance, but even in far-off Greece where in Lower Pliocene rocks of Pikermi near Athens they are entombed. *Hipparion whitneyi* reached a height of 40 inches or 10 hands, while *Hipparion gracilis* of Pikermi stood 44 inches at the shoulder.

Pliocene.—Pliocene time was one of great unrest; conditions were becoming more and more severe, prophetic of the Glacial period, new land-bridges arose where none had existed for ages, and we find great consequent faunal interchanges recorded. It is not remarkable therefore that *Hipparion* reached the Old World just as the true elephants made their first appearance in the New.

Plesippus, the ninth stage, was formerly known from very fragmentary material, but in 1924 Messrs. Matthew and Simpson found two skeletons at Mount Blanco, Texas, that present almost every detail. The size and general proportions are about those of the Arab horse but the feet are much smaller. The teeth are an advance over those of *Pliohippus* in having a longer, less curved crown, as in *Equus*, otherwise they are more *Pliohippus*-like. There is no trace of the lateral toes, while the skull is *Equus*-like, having almost entirely lost the facial pits.

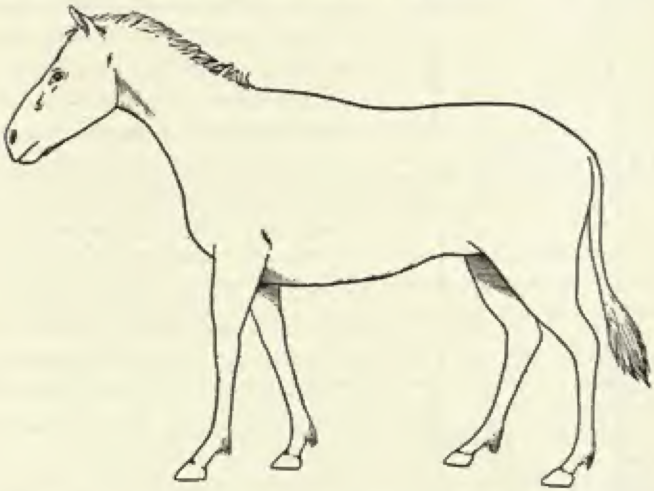


FIG. 229.—Restoration of the first one-toed horse, *Pliohippus*. (After Lull.)

Another notable Pliocene event was the appearance for the first time in geological history of true horses in South America, whither they went in company with the dibelodont mastodons. The South American Pliocene horse was *Hippidion* (Fig. 232), evidently a derivative of *Protohippus* but differing in having short, stout rather than slender, one-toed feet. The teeth are like those of *Pliohippus*, but the skull differs remarkably in the extremely long, slender nasal bones which, together with the great size of the head, must have given the creature a very peculiar cast of countenance. *Hippidion*, which had attained a stature of 12½ hands, lingered into the Pleistocene, where it became *Onohippidium*, a creature but recently extinct if one may judge from the fresh-looking horny hoofs preserved in certain Patagonian caves.

The modern horse, *Equus*, the tenth and final stage, first appears in the Upper Pliocene beds of Eurasia and North America and represents the culmination of the race. The feet are one-toed, but with well-developed splints of the second and fourth digits still remaining. In some individuals these are fused with the cannon-bone; in others they are free. The teeth are long columnar structures of intricate enamel pattern, admirably adapted to their owner's needs, and the animal has attained the maximum stature consistent with fleetness.

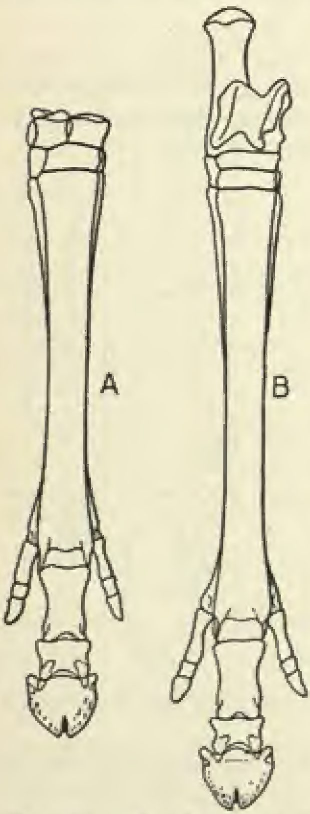


FIG. 230.—Hand (A) and foot (B) of three-toed desert horse, *Hipparion*, Pliocene, North America and the Old World. One-fourth natural size. (After Lull.)

Pleistocene.—A number of extinct species of *Equus* are recorded, principally from the Pleistocene of both North and South America and the Old World. Of these the best known is Scott's horse, *Equus scotti* (Fig. 233), from the staked plains (Llano Estacado) of Texas. This species, of which a number of perfect specimens have been found, was discovered at Rock Creek, Texas, in 1899 by an expedition from the American Museum of Natural History. Thirteen years later a party from Yale reopened the quarry and secured several more specimens, one of which (Pl. XXIV) is now mounted in the Yale Museum. It is of an animal about 15 hands in height, having somewhat the proportions of a western broncho, but with a very large head and with teeth greater than those of a modern dray horse, although very similar in pattern. Horses of this or related species, some smaller, others larger, are extraordinarily abundant wherever the earlier Pleistocene deposits

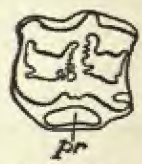


FIG. 231.—Upper tooth of *Hipparion*. *pr*, free protocone. (After Lull.)

are found in North America, and they evidently survived the first glacial advance, but shortly afterward, why we cannot tell, they

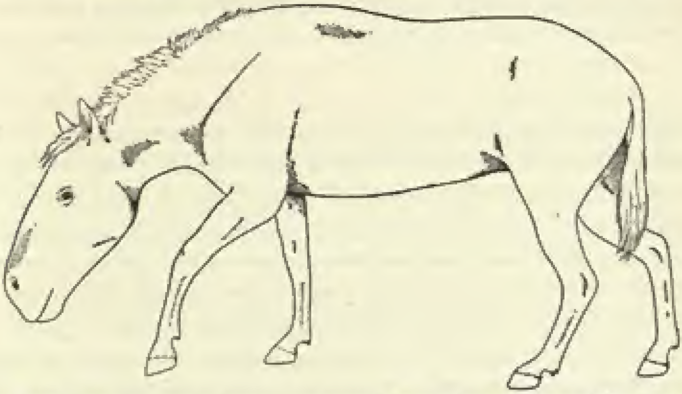


FIG. 232.—Restoration of the one-toed Pampas horse, *Hippidion*, Pleistocene, Argentina. (Redrawn from Scott.)

became extinct not only in North but in South America as well. This apparently was also true of Europe but in Asia and Africa the race found sanctuary, otherwise the horse would be included

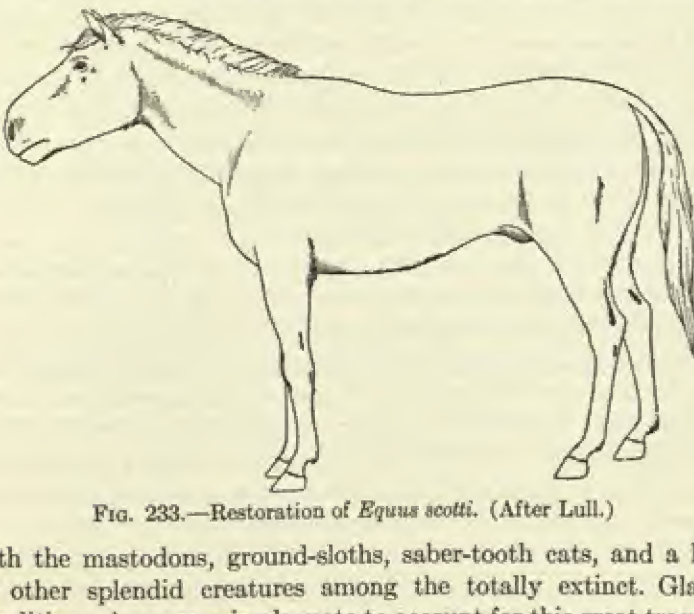


FIG. 233.—Restoration of *Equus scotti*. (After Lull.)

with the mastodons, ground-sloths, saber-tooth cats, and a host of other splendid creatures among the totally extinct. Glacial conditions alone seem inadequate to account for this great tragedy,

for not only did the hand of death bear heavily upon the equine herds within the limits of the ice belt, but far beyond, to the uttermost confines of the western hemisphere. That no permanent change of environment occurred to render the earth unsuitable for these creatures is evident from the amazing way in which the few imported horses liberated by the Spanish Conquistadores multiplied and spread, giving rise to the great herds of wild mustangs in both North and South America. We look naturally therefore for some other cause of extinction and the one of all theories that seems most plausible is the bringing in by migrating animals of insect-transmitted disease, such as the sleeping sickness of Africa or the Surra disease which attacks domestic horses in India. A further discussion of this problem has been given in Chapter XVII on parasitism and degeneracy. So far as we know now such an extinction cause is incapable of proof, unless it shall be found that these diseases produce a recorded change upon the bones themselves, for of course the soft anatomy of fossil horses is utterly beyond our reach for direct study.

Living Horses.—Several species of horse-like animals are yet alive in their wild condition in Asia and Africa, all of those of Europe and the Americas being either domesticated or feral, that is, of domestic ancestry. Of the true horses but one wild type remains, the Mongolian or Przewalski horse, the tarpan of the Gobi Desert of central Asia and the neighboring regions. It is a small animal, standing but 12 hands, of a yellow dun or "buckskin" color, with black mane, tail, and legs, and a white muzzle. There is no forelock, the mane is short and erect, and there is a decided beard beneath the relatively large head.

At least three other primitive types of true horses are living under the fostering care of mankind, and these or an admixture of them constitute our various domestic breeds. Of them the first is the Celtic pony—pale buff, mouse gray, or even brown, with a large forelock and tuft beneath the jaw, a light colored mane and tail, but with a certain admixture of black hairs. There is long bushy hair at the base of the tail. This horse is also characterized by a short face, broad forehead, slender legs, and small hoofs, and is found from Iceland to western Norway.

The second form is the Norse yellow dun or forest pony, related evidently to the Mongolian horse, but larger, stockier, and with fuller mane and tail. In some instances there is a dark stripe down

the back and traces of barring on the legs. The face is longer and the hoofs relatively larger than in the Celtic horse. The Norse pony is the main ancestral stock for the ordinary domestic horses of northwestern Europe. The changes may be due to domestication or to the infusion of Arab blood.

The last great type is the southern horse or barb, the Arab or thoroughbred, *Equus africanus*. The color of this creature is bay, sometimes gray, with black points and often with a white star on the forehead and one or more white legs. It has a small head and slender, graceful limbs, and possesses great docility and spirit.

Nearest the true horse comes the kiang, *Equus kiang*, of central Mongolia and Turkestan. This creature is not an ass although ass-like in many ways. It stands 12½ hands, the ears are horse-like and the hoofs broad, especially in front. The tail tuft is large and there is the rudiment of a forelock. In winter the color is grayish, in summer chestnut, with no striping.

The zebras are exclusively African and are of course characterized by a very conspicuous striping when seen out of their natural surroundings. They are, nevertheless, generally reported to be protectively colored when in their appropriate habitat, although this is a subject upon which Colonel Roosevelt had much to say, as he believed that the theory of protective coloration has been considerably overdrawn (*African Game Trails*, Appendix). There are two well defined species of zebra living, while a third, the quagga, was so recently exterminated that mounted skins may be seen in certain museums. The plains or Burchell's zebra is somewhat variable in the coloring but always lacks the cross-striped rump, the so-called "gridiron" of the true or mountain zebra. The former is still numerous, in fact it is said to be the second big game animal of the world in point of numbers. The mountain zebra, on the other hand, is becoming so rare that it is protected by law. It is more nearly related to the ass and has longer ears, narrower hoofs and a scantier tail tuft than the Burchell species.

The ass, *Equus asinus*, is domesticated the world over, in fact its subjugation by mankind long antedates that of the horse. Asses are still wild in the tropics of Africa and are gray at all seasons, with a dark back stripe. When wild the size is medium to large, ranging from 11 to 12¼ hands at the shoulder. The hoofs are small and narrow and the fore pair are no larger than the hinder ones. There are two varieties, the Nubian ass, which has a trans-

verse shoulder stripe, and that of Somali, which lacks the shoulder stripe but has barring on the legs. The domestic variety is typical of the Nubian form.

Horses and Man

Mankind owes a profound debt of gratitude to the horse, first in savage days as an easily obtainable food, later as a partner in his labors without whose aid human progress toward a higher civilization would have been retarded immeasurably. It has been thought by some that the condition of semi-barbarism of the North American Indians, really a race of great potentiality, was in part due to the premature extinction of the American horses.

There is no record of the association of man and the extinct horses of America, but during prehistoric times in Europe, before the extinction of the mammoth, we find records of the association of the horse and man in the form of mural decorations on the walls of caverns. It is interesting to note that at least three types of horses are shown by the Paleolithic artists: one a small-headed form resembling in this regard the Arab of to-day, another large-headed, with the erect mane and beard typical of the living Przewalski horse, and a third which in contour closely resembles the Norse or forest pony. The presence of bridle-like markings on the head of one horse has been taken as an indication of domestication on the part of the prehistoric peoples. One finds, however, no trace of a drawing of a man on horseback or other use of the animal as a beast of burden and the idea has been advanced that possibly because of its extreme docility it may have been occasionally easier to lead home a captured horse to the slaughter than to carry home the meat.

One of the most remarkable prehistoric encampments, not in caves but in the open air, is at Solutré in Saône-et-Loire, France. Here there was a fine southern exposure sheltered on the north by a steep ridge. Encircling the south side was a kind of protective wall formed almost entirely of the bones of horses to the estimated number of 80,000 individuals! Such a wholesale slaughter of course extended over a long period of time, but might readily have been an important factor in local extermination when aided by the weakening effects of disease.

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CHAPTER XXXVII

CAMELS

The camels are another group of animals whose phylogeny has been very clearly demonstrated by the fossil evidence, the perfection of the record being second only to that of the horses. Add to this the fact that they are throughout almost their entire evolutionary career exclusively North American forms, and their title to a high place in our interest is complete.

Place in Nature.—As the horses were representatives of the Perissodactyla or odd-toed ungulates, so the camels belong to the other great group of hoofed forms, the even-toed Artiodactyla. The latter, now largely eliminated from the western world, are still comparatively numerous in Africa and Eurasia, where at least 250 distinct species are known as against 34 for the Americas. That the Artiodactyla were formerly much more abundant, especially in North America, is forcibly brought home to every collector of fossil vertebrates in the West.

The principal points of agreement of all artiodactyls are: the axis of the foot lies *between* digits three and four rather than within digit three as in the perissodactyls; hence the two digits, one on either side of the axis, are symmetrical and the number two is the irreducible minimum. While there are normally an even number of digits, the peccaries, *Tayassu*, have three remaining in the foot, and a five-toed ancestral artiodactyl is conceivable, for the oreodonts retained a well defined vestige of the first digit of the hand. Another artiodactyl characteristic lies in the astragalus, the ankle bone which articulates with the tibia or shin. In common with that of the perissodactyls, the upper or tibial facet is pulley-shaped, but in the latter the distal facet is flat, thus permitting no movement between it and the succeeding tarsal bones. In the artiodactyls, on the contrary, the distal facet is curved in such a way that a double tarsal joint is formed. This type of astragalus, a very resistant bone, is an extremely common fossil and is absolutely diagnostic of the group.

The molar teeth are invariably one of two sorts or a combination of them. The crown either bears conical cusps (bunodont, Gr. βουνός, hill, and ὀδούς, tooth) as in the swine, or the cusps are crescentic (selenodont, Gr. σελήνη, the moon), the latter sort being typical of the cud-chewing forms of ruminants. Certain ancient types (anthracotheres) had buno-selenodont teeth of a transitional character. The teeth may be short-crowned or, in the grazing ruminants, deep-crowned as an adaptation to abrasive food; they never, however, reach the degree of perfection seen in the true horses.

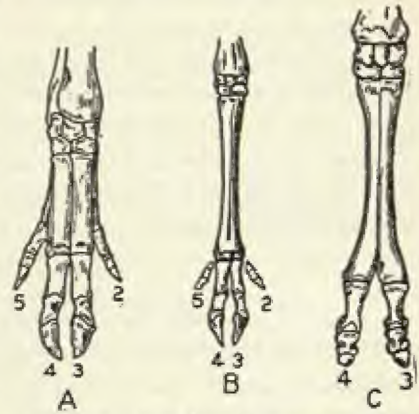


FIG. 234.—Fore feet of artiodactyls. A, pig, *Sus scrofa;* B, red deer, *Cervus elaphus;* C, camel, *Camelus bactrianus.* To show progressive reduction of lateral digits. (After Flower.)

Artiodactyls are apt to possess weapons, either tusks, which are modified canine teeth, or horns or antlers of various sorts and degrees of development, or rarely both.

A classification of the artiodactyls adapted from Romer is:

Suborder Suina (swine-like)
  Family Suidæ (swine)
    Entelodontidæ (giant swine)
    Dicotylidæ (peccaries)
    Hippopotamidæ (hippopotami)
Suborder Ruminantia (cud-chewers)
  Family Camelidæ (camels and llamas)
    Oreodontidæ (oreodonts)
Infraorder Pecora (true ruminants)
  Family Cervidæ (deer)
    Giraffidae (giraffes)
    Antilocapridæ (prong-bucks)
    Bovidæ (antelopes, sheep, cattle, etc.)

Thus it will be seen that the camels occupy an intermediate place within the order; they are, however, an isolated group, as their connection with the others is not yet clear.

Camel Characteristics.—The characteristics of living camels are as follows: The limbs are long, and two-toed; the metapodials, which are fused to form a cannon-bone, diverge distally, and the keels which serve to restrict the lateral movement of the digits in other forms are here very limited. Hence the secondarily digitigrade foot is yielding as an adaptation to desert sands. The feet are, moreover, provided with one or two cushion-like pads, hence the name Tylopoda (Gr. τύλη, cushion and πούς, foot). The stomach is three-chambered; there is a primitive type of placenta; and the red blood corpuscles are elliptical instead of circular in outline, which makes the group absolutely unique among living mammals.

Living Genera

Camelus

There are but two living genera, each of which includes a like number of species—four altogether extant—one, *Camelus*, being confined to the Old World, while the other, *Lama* or *Auchenia*, is characteristic of the New.

The two species of camel are *Camelus dromedarius*, the one-humped Arabian camel or dromedary, and *C. bactrianus*, the two-humped Bactrian camel of central Asia. The two species will interbreed and the consequent hybrid or mule camel possesses the one hump of the dromedary and the brown shaggy coat of the Bactrian parent. The progeny of a male Bactrian and female Arabian camel is preferred to either of the pure breeds.

The camel has rightly earned its name of "ship of the desert," for practically all of its peculiarities are but an adaptive response to the harsh conditions of that inhospitable environment. Many of these adaptations have been mentioned in Chapter XXIV, but they must be reviewed and brought together in order that the evolution of their owner's ancient lineage may be better appreciated. As in the horse, two directions of adaptation stand out sharply—that of speed, ever a desert requisite, and that of teeth, for the harsh and scanty herbage. The other characteristics the horse does not possess, for they are the direct outcome of desert life.

Speed.—Cursorial characteristics are well shown in the length of limb, reduction of digits, of ulna and fibula, and in the limitation of the range of movement of the limb joints. The feet, however,

have retrogressed in that they are no longer unguligrade but digitigrade, for almost the entire length of the phalanges, except for the intervening pad, lies flat upon the ground. The hoofs are reduced to nail-like structures and the whole yielding foot, with its absolutely silent tread, is admirably designed to support the animal on the shifting desert sands. The foot retrogression somewhat diminishes the extreme length of limb, but this is to a certain

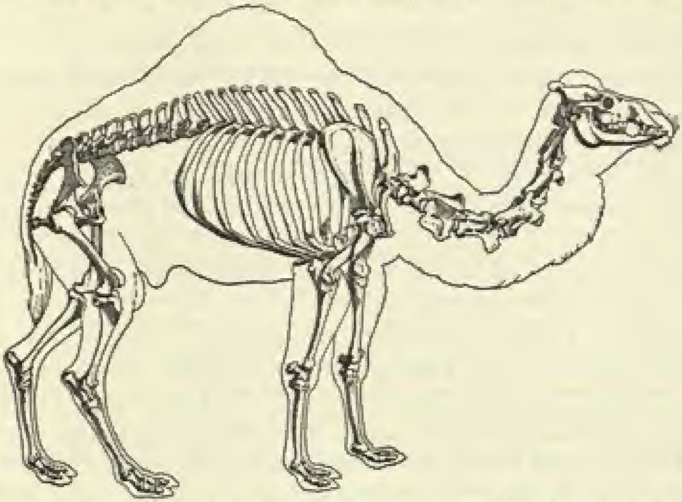


FIG. 235.—Skeleton with bodily outline of camel, *Camelus dromedarius*. (After Pander and D'Alton.)

extent compensated for by the fact that the thigh is freer from the body than in other ungulates and thus the length of stride is increased.

Teeth.—The teeth of the camel have suffered a reduction in numbers, to 34, instead of the normal 44. There is but one upper incisor left on either side and it is more canine- than incisor-like. The lower incisors, on the other hand, are all present, more or less spatulate and procumbent, and the canine is somewhat similar and functions as an incisor. Behind the canine comes a short diastema and then a recurved, tusk-like premolar which has assumed the discarded form and function of the canine. This is followed by a longer toothless area, and the four cheek teeth—the fourth premolar and the three molars—form an efficient compact grinding mechanism, of long-crowned but, as compared with the horse, relatively simple teeth.

Hump.—The hump which forms so very characteristic a camel feature consists of a conical mass of gelatinous fat when the animal is well fed, is nourishment stored against a time of scarcity, and can be drawn upon during the passage of the desert. Whether or no any of the extinct camels possessed such an organ we cannot tell, as it is entirely superficial and leaves no impression upon the skeleton. The hump becomes flaccid and falls over on one side in an exhausted camel.

Water Reservoirs.—Another desert characteristic is the development of water reservoirs in the walls of the stomach (properly the paunch or rumen). These are small flask-shaped cavities, each with a constricting muscle at its mouth, so that when the stomach is filled with water the muscles relax automatically, allowing the water to enter the cavities, while that which remains is absorbed into the system. In time of water scarcity the stored liquid is allowed to trickle out into the stomach and is thence available for the impoverished blood.

Senses.—The proud carriage of the head, which is held horizontally some nine feet from the ground, protects the eyes from the reflected heat and the eyes and nostrils from the sand. The sense organs are still further protected, the eyes by long lashes, the ears by hair, and the nostrils by being closable, like eyelids. The creature is keen of sight, but what is still more necessary, the sense of smell is very well developed so that water may be detected a long way off.

Mentality.—Mentally the wild camels are sagacious, as the brain is large and well convoluted, but the domesticated ones are so stupid that their bad traits are notorious.

Thus Palgrave observes (in Flower and Lydekker): "If docile means stupid, well and good; in such a case the camel is the very model of docility. But if the epithet is intended to designate an animal that takes an interest in its rider so far as a beast can, that in some way understands his intentions, or shares them in a subordinate fashion, that obeys from a sort of submissive or half-fellow feeling with his master, like the horse or elephant, then I say that the camel is by no means docile—very much the contrary. He takes no heed of his rider, pays no attention whether he be on his back or not, walks straight on when once set agoing, merely because he is too stupid to turn aside, and then should some tempting thorn or green branch allure him out of the path, continues to walk on in the new direction simply because he is too dull to turn back into the right road. In a word, he is from first to last an undomesticated and savage

animal, rendered serviceable by stupidity alone, without much skill on his master's part, or any coöperation on his own save that of an extreme passiveness. Neither attachment nor even habit impress him; never tame, though not wide-awake enough to be exactly wild."

As beasts of burden, however, camels are entitled to respect, as one can carry 500 to 800 pounds, and their endurance is phenomenal, the Arabian breed known as the "Heirie" camel traveling from 125 to 150 miles a day for eight to ten days at a time. The distance from Tunis to Tripoli is 600 miles, yet a single camel has carried over that route a burden of rider and gear weighing not less than 250 pounds, in four days—an average of 150 miles a day!

Uses.—Alive, camels are used as beasts of burden, for their milk, and for the shed hair which is spun and subsequently woven. Dead, the flesh is used as food, the hides for leather, the hair for fabrics, and even the bones are utilized. Their importance to mankind, especially to the nomads of the East and to traders between great cities, can hardly be estimated. Necessities of war have developed means of desert transportation in the form of tractors and other motor vehicles, as well as airplanes. To what extent such machines will be used to aid travel and commerce in time of peace remains to be seen. With nomadic peoples, however, who do not care for or possess means of mechanical transportation, the camel must still be highly important.

It is interesting to note that, while the American Museum expeditions to Mongolia have an adequate fleet of motor cars, they also have a supporting train of camels, which carries in gasoline and other supplies and brings specimens out.

There are wild camels in remote Turkestan, the desert of Lobnor, and in Spain, but some are certainly feral, *i. e.* of domestic ancestry, and all are probably so, as there are ruins of ancient cities in the Asiatic portion of their range of which the very traditions have vanished and to whose departed citizens the ancestors of these camels may well have belonged. It is highly probable that they have not existed wild for thousands of years.

The area of servitude includes Arabia, Persia, India, all of the country from North Tartary to the confines of China and the coast of the Persian Gulf, and the Canary Islands and Africa north of the Sahara. There were none in Africa, however, until the third century of our era. Attempts to naturalize them in Australia and

North America have been made, but the lack of success in America has not been due to the climate or other physical conditions of their ancestral home, but rather to their unfavorable reception by the Americans, who greatly preferred the highly serviceable, cheaper, and more tractable burro.

Lama (*Auchenia*)

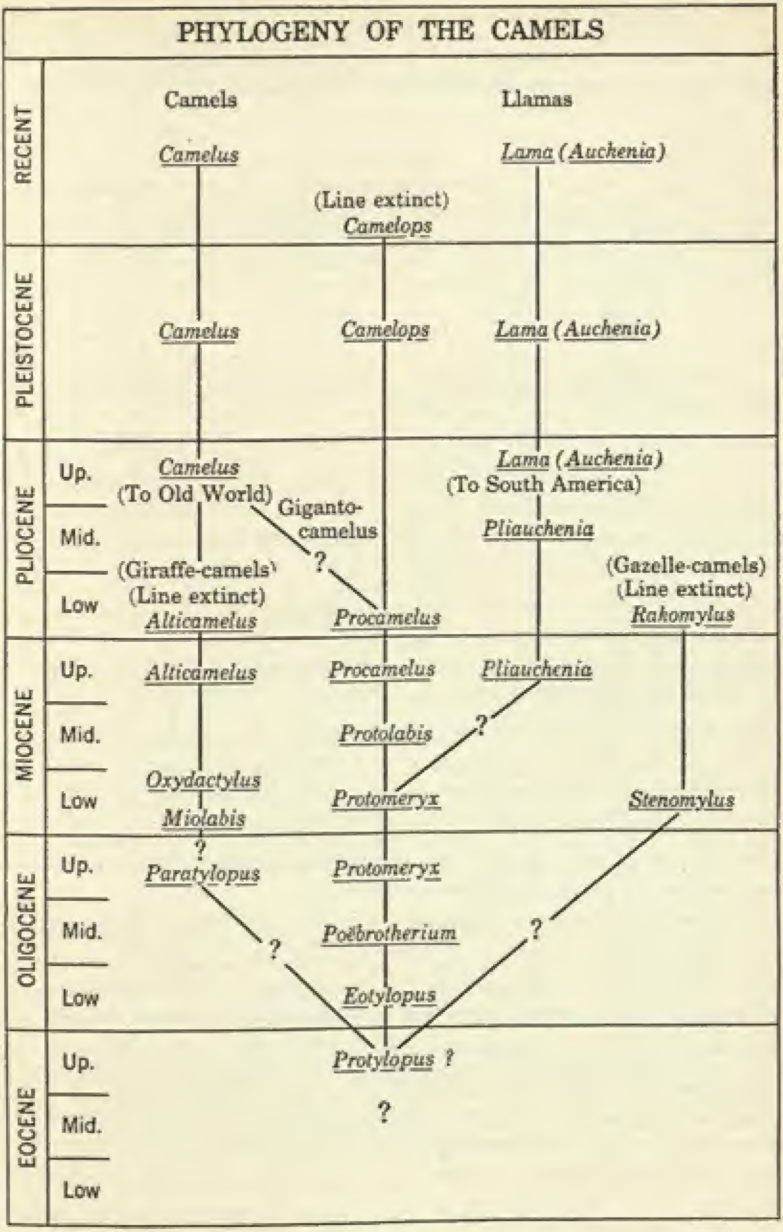
Characteristics.—The South American genus, *Lama* (= *Auchenia*) (Fig. 236), includes two wild species, the guanaco, *L. huanacus*, and the vicuña, *L. vicunia*, and their domestic derivatives, the llama and alpaca. These creatures are of much smaller stature than the camel and lack the characteristic hump of the latter. The feet are narrow and the toes more distinctly divided, with two pads beneath instead of but one. The hair is woolly as a protection from the cold of their mountain home, for instead of being adapted to sandy desert conditions, although their structure shows a desert ancestry, they are upland animals, which may well account for their attainment of South America along the isthmian land-bridge, to the exclusion of the true camels.

FIG. 236.—Guanaco, *Lama huanacus*, living, South America. (After Scott.)

Range.—The *Lama* range is along the west side of South America from the equator to Cape Horn. Domesticated, they have their uses similar to those of their Asiatic cousins, as beasts of burden, and for the flesh, hides, and wool. They have the distinction of being America's only contribution to the list of mammals domesticated by mankind, but although their local importance may be great, they have by no means contributed to human progress and well-being to the extent that the camels have.

EVOLUTIONARY CHANGES

These are in a way comparable to the changes undergone by the horses, with the exception of the secondary retrogression of the feet. To summarize briefly, the changes are as follows: Increase in


PHYLOGENY OF THE CAMELS
RECENT
PLEISTOCENE
PLIOCENE
MIOCENE
OLIGOCENE
EOCENE
Up.
Mid.
Low
Camels
Llamas
Camelus
Lama (Auchenia)
(Line extinct)
Camelops
Camelus
Camelops
Lama (Auchenia)
Camelus
(To Old World)
Gigantocamelus
Lama (Auchenia)
(To South America)
Pliauchenia
(Giraffe-camels)
(Line extinct)
Alticamelus
?
Procamelus
(Gazelle-camels)
(Line extinct)
Rakomylus
Alticamelus
Procamelus
Pliauchenia
Protolabis
?
Oxydactylus
Miolabis
Protomeryx
Stenomylus
?
Paratylopus
Protomeryx
Poëbrotherium
?
?
Eotylopus
Protylopus ?
?

stature from the size of a western jack-rabbit to one much greater than the huge Bactrian camel of today. Loss of lateral digits, of which not the least vestige remains. Elongation and fusion of metapodials to form the very characteristic, distally spread cannonbone. Retrogression from unguligrade, deer-like feet to digitigrade, broadening of phalanges, development of foot-pads with the coming of desert conditions in the Pliocene, reduction of number of teeth, elongation of teeth in the grazing phylum (see Fig. 237).

Phylogeny

North America is, as we have seen, the evolutionary home of the camel family, and, as Matthew (1915) says, "Its ancestral stages can be very fully and exactly traced in the western formations, as far back as the Upper Eocene, below which they are merged with the ancestry of other groups. They are unknown in any other continent until the Pliocene, when they invaded South America and Asia and Africa, surviving in those continents to-day, although extinct in North America since the Middle Pleistocene."

Why the ancestral camels failed to migrate to the Old World before the Pliocene, when the horses repeatedly made the journey, is somewhat obscure unless, as Matthew (1915) again suggests, their center of radiation was further south, for, as he says, "The center of dispersal would appear to have been in this continent,—how far to the north we have no means of estimating; but the exceptional directness of the phylogenetic series as represented by our western fossils indicates, in my opinion, that these fossils lived in or close to the racial dispersal center."

Eocene.—Camels are unknown until Upper Eocene time when the first possible ancestor of the line appears in *Protylopus* (Fig. 237). This small creature was no larger than a jack-rabbit, and had 44 teeth, those in each jaw forming a continuous series, the canine being only slightly enlarged. All of the molars were low-crowned. The skull with its narrow face suggests that of the existing forms, but the bony orbit was incomplete behind. The fore limbs were considerably shorter than the hind so that the back sloped upward toward the rump. The ulna was entirely separate from the radius and the fibula was complete. The hand had four functional digits but the lateral toes of the foot were greatly attenuated although still complete. *Protylopus* is from the

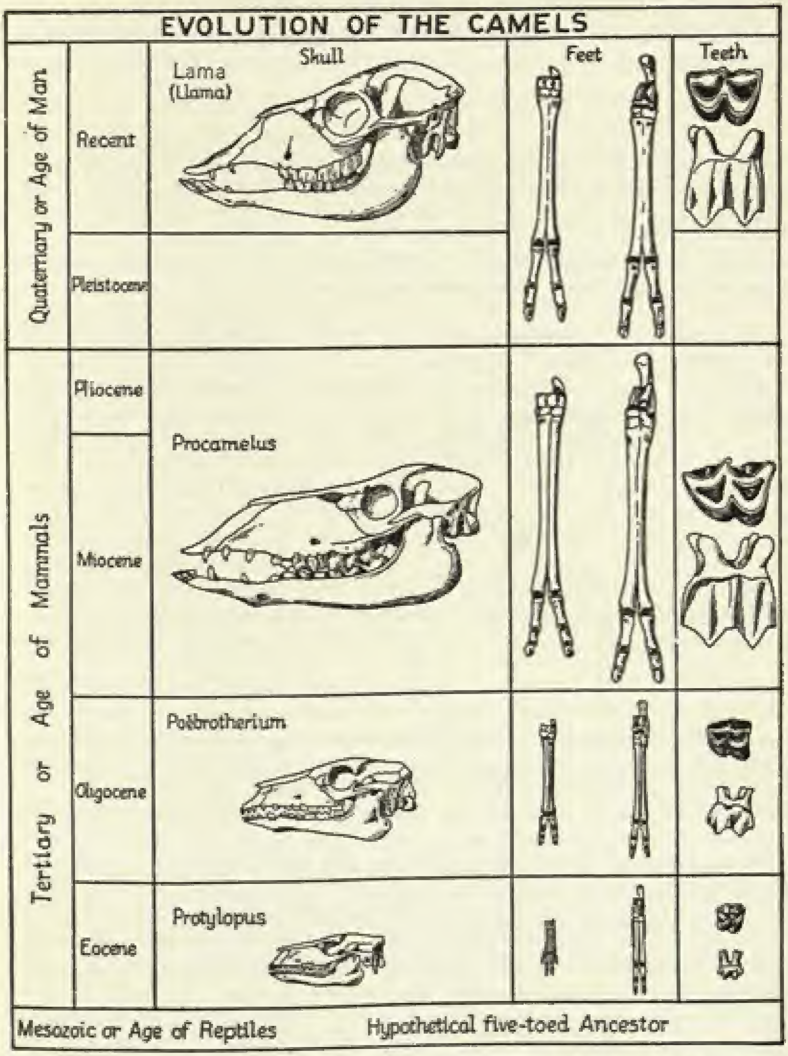


FIG. 237.—Camel evolution as indicated by the skull, feet, and teeth. (Modified after Scott.)

Uinta stage and is thus contemporaneous with the horse *Epihippus*, to which it is comparable in degree of evolution.

Oligocene.—During the Oligocene, camel-like animals increased in numbers so that they must have been a very characteristic though rare element in the fauna of that time. This is especially true of *Poëbrotherium* (Figs. 237; 238), the remains of which are abundant in the "Big Bad Lands" of South Dakota, whence they range across Nebraska into Colorado and west to the John Day valley of Oregon. As *Protylopus* parallels *Epihippus*, so *Poëbrotherium* resembles the contemporary *Mesohippus* in the degree of its evolution. *Poëbrotherium*, like *Mesohippus*, attained the stature of a sheep, but the former was more lightly constructed than the sheep, with relatively longer limbs and neck and with a small tapering skull. The teeth are still forty-four as in *Protylopus* and the incisors and canines are more typical of mammals in general, not the procumbent, spatulate structures of later cameloids.

Fig. 238.—Restoration of ancestral camel, *Poëbrotherium labiatum*, Middle and Upper Oligocene, North America. (Restored from a skeleton in the Amherst College Museum.)

The grinding teeth of the upper jaw are short-crowned, while the lower molars have begun to elongate. The jaws are very slender. The limbs show a marked digital reduction both in the hand and foot, in that small nodules only are present as the last vestiges of the lateral toes. The ulna has coalesced with the radius and only the two ends of the fibula remain. The hoofs are deer-like. The Upper Oligocene *Protomeryx* differs from *Poëbrotherium* mainly in the complete encircling of the orbit by bone.

Miocene.—During the Oligocene there began an initial divergence into at least three phyla which became well-defined groups during the Miocene, paralleling once more the equine evolution. Of these the grazing camels, which were the main line leading to the

modern representatives of the race, include the Lower Miocene *Protomeryx* and the Upper Miocene *Procamelus*.

The former, *Protomeryx*, still possessed the full quota of teeth, but the grinders show a decided deepening tendency as an adaptation to the abrasive grasses. The feet had two digits and possessed pointed hoofs like those of the deer.

In *Procamelus* (Fig. 237) we find the first tooth reduction, in that the first and second upper incisors are lost in the adult stage. The feet have advanced, for the metapodials are beginning to fuse to form the cannon-bone. The first desert adaptation is shown in the foot bones in this genus which imply the presence of a padded foot. In size *Procamelus* must have exceeded the dimensions of the modern llama.

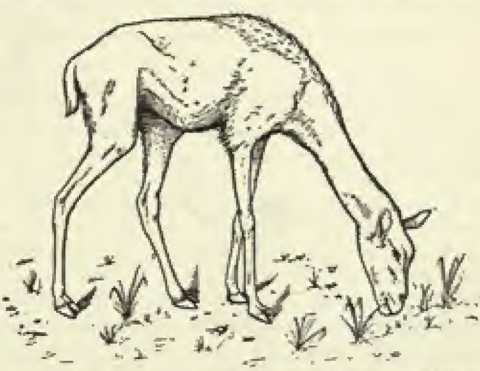


Fig. 239.—Gazelle camel, *Stenomylus*, Miocene, Nebraska. (Redrawn from Scott.)

A very notable fossil locality in western Nebraska, of Lower Miocene age, has yielded a large number, some forty or more, of a slender camel-like form known as *stenomylus* (Fig. 239), the gazelle-camel, delicate in its proportions and much smaller than any of its contemporaries. Its Oligocene ancestry has not yet been traced and except for the early Miocene *Rakomylus*, the inference is that the line soon became extinct. It has an apparent anomaly in its dentition, as there are ten incisor-like teeth in the lower jaw, six true incisors, and in addition the canines and first premolars which have assumed a similar form and function. The low-crowned molars imply a browsing habit. The head is small, the neck long and delicately built, and the limbs and feet extremely slender, with very thin-walled bones. There are but two toes on each foot and the metapodials are not fused. Apparently fleetness was *Stenomylus*' only defense, which may have accounted for its brief racial career. The known specimens, of which a group of two individuals is mounted at Yale, are almost without exception from a single quarry, where they occur in profusion, some dis-

membered, others in completely articulated condition as though the carcasses had drifted downstream in time of flood, to be caught in the backwater of some large cove and buried by sediment. This is in accord with the belief of the discoverer, Professor Loomis, based upon anatomical grounds, that *Stenomylus* was an upland form. The only associated remains other than those of the camel found in the quarry pertain to a large wolf-like creature known as *Amphicyon* (=*Daphænodon*) *superbus*, probably one of the forms which preyed upon the camels.

The name giraffe-camels does not imply relationship with the giraffes, which, so far as known, with one exception have been confined exclusively to the Old World, but is applied to creatures which from community of habit converged very strongly toward the existing giraffe in size and proportions. Two Miocene genera have been discovered which pertain to this family, and in the aberrant Oligocene *Paratylopus* we recognize the first recorded ancestor of the group. In the Lower Miocene the representative is *Oxydactylus* (Fig. 240), remains of which have been collected in eastern Wyoming and western Nebraska. This form is much smaller than its successor, *Alticamelus*, and has a shorter neck and limbs. The metapodials do not fuse to form a cannon-bone and the hoofs are sharp-pointed and deer-like, with little indication of the sand-adapted feet of the later camels. The teeth of *Oxydactylus* are rather short-crowned, as though fitted for browsing rather than for grazing, and they are yet 44 in number.

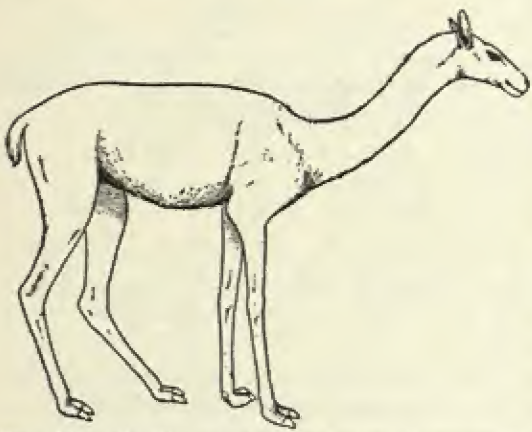


FIG. 240.—Giraffe camel, *Oxydactylus*, Miocene, Nebraska and Wyoming. (After Scott.)

Alticamelus of the late Miocene and early Pliocene, although clearly derivable from *Oxydactylus*, is much further advanced in

more than one way, for we find that the feet show the same desert adaptation that its contemporaries of the grazing phylum do—cannon-bone, depressed phalanges, and indications of pads—a remarkable instance of convergence, the like response of unrelated phyla to a similar climatic change. *Alticamelus* was a very large animal, although the head was small and the teeth, like those of its predecessor, are low-crowned. The neck and limbs are very long as in the giraffe and were probably, as with the latter, an adaptation to permit the animal to browse upon the otherwise inaccessible foliage of high and thorny shrubs like the African mimosa, which forms the staple of giraffine diet. But while the result of this remarkable convergence was to produce the same effectiveness for such a method of feeding, the way in which it was brought about was not the same.

Pliocene and Pleistocene.—Pliocene camels belong to the main grazing phylum and are the direct descendants of the Miocene *Procamelus*, from which they hardly differ at all. The Pliocene and Pleistocene camels *Camelops* and *Eschatius* are not very well known, owing largely to the fragmentary character of the material thus far collected, with the exception of fine skeletons of *Camelops hesternus* from the Rancho la Brea (Pl. XXV). The Pleistocene camels, however, were very numerous and future discoveries are sure to bring better specimens to light. Not all of the Pleistocene forms are true camels in the sense of being like those of the Old World, but are cameloid creatures, possibly more llama-like in appearance. Some of them attained an enormous size, as certain bones preserved at Yale are half again as large as equivalent elements from a Bactrian camel.

Typical camels, of the genus *Camelus*, differ from *Procamelus* in the further loss of one premolar in the upper and two in the lower jaw, and this genus is apparently the first to brave the cold of the northern route and pass to the Old World, presumably by way of the Bering land-bridge, for we have the first recorded remains of it in the famous Siwalik formation (Lower Pliocene) of India. The two Indian species of *Camelus*, *C. sivalensis* and *C. antiquus*, show a peculiar tooth character found in the New World llamas but lost in the living camels, indicating that in some respects the New World types are the more primitive. Fragmentary *Camelus* fossils have been found in the Pleistocene of southern Russia and Roumania, and in Algeria not far removed from the

living habitat of the race. The extinction of the North American camels is as inexplicable as that of the horses, and may well have been due to the same unknown complex of causes.

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CHAPTER XXXVIII

SOUTH AMERICAN MAMMAL RADIATION

The South American fauna presents an extremely interesting example of what may happen in a large and varied area during a long period of isolation. The continent of South America is today, owing to the existence of the Panama Canal, entirely isolated by water from the rest of the world. So it was for long periods of geologic time, due of course to natural causes. As a consequence there developed, during these periods of isolation, a most amazing local fauna, the members of which differ markedly from the more familiar creatures inhabiting the rest of the globe.

Paleogeography.—Not only is South America vast, extending as it does from 10 degrees north of the equator to 55 degrees south, but it varies greatly in climate as a consequence of its latitudinal range, as well as its topography. Moreover, it is so completely surrounded by water that its isolation by the forces of nature was most readily accomplished. Of the former land connections there have been several opinions, but the authority of Charles Schuchert is taken as final, for it is backed by years of the most painstaking accumulation of data and by very judicial interpretation.

Three possible lines of communication have existed in the past: that with North America, though not necessarily by way of the present Panamanian isthmus; one from the southern extremity to Antarctica and thence to Australia; and the third across what is now the South Atlantic to Africa.

The evidences of these old-time connections are in part geological but more largely biological and paleontological and are based upon present and past distribution of animals both by land and sea. Manifestly similar and closely related terrestrial animals, vertebrate or invertebrate, normally incapable of overseas migration, point to the existence of land-bridges as migratory routes. The same is true of strictly fresh-water fishes. Marine creatures whose home is on the continental shelf can, on the other hand, only migrate where shores are continuous. Thus, where Atlantic and Pacific marine animals are similar, it points to aquatic continuity,

by way of a strait or other body of water, and therefore to the absence of land connection, whereas dissimilar marine forms imply land continuity, which would of course serve as a sea barrier. It is by the accumulation of evidences such as these, not only in existing but in fossil forms, and by the careful plotting of the occurrences on successive geological maps that the old-time shore lines are indicated, for they must lie somewhere between the points of occurrence of land and marine animals of contemporary age.

The evidence may be summarized as follows:

Between the Americas there was connection during the Mesozoic, broken in Eocene time (Upper Eocene, according to Schuchert; Matthew, however, says Paleocene, otherwise the carnivores would be creodonts and not marsupials), reëstablished in early Pliocene, and practically continuous until the present day, except for the canal. Thus the period of isolation lasted during part of the Eocene, all of the Oligocene and Miocene and into the Pliocene, a duration of perhaps fifty million years.

After its reëstablishment in the Pliocene the land-bridge was evidently much broader than the present Isthmus of Panama, but soil had to form as a result of rock disintegration, and the establishment of vegetation had to precede the migration of terrestrial mammals, which in the long run depend upon the plants for food.

With Australia via Antarctica the communication, if it actually existed at all, was again an ancient one and was also severed very early in the Eocene and has never been reëstablished. The same was apparently also true of the African connection. Evidence speaks of the existence of a vast equatorial continent, extending from South America across the South Atlantic to Africa, and again to India, the East Indies, and Australia, including part of what is now the Indian Ocean. This great area has been named Gondwanaland, and, while its former existence is denied by good authority, the evidence for it is strong and well founded. Some question has arisen as to the date of its final severance, but Schuchert's belief is that it began to break up toward the close of the Cretaceous, so that by Tertiary time all chance of migration by this route had ceased. Matthew's argument also holds here.

These old-time connections of course afforded paths of migration for terrestrial animals, both vertebrate and invertebrate, and from some one or more of them must have come the ancestors of the peculiar South American fauna, except such elements as

were strictly native in origin. The edentates among mammals seem to be the only order which can be referred to this latter group, however, as they alone show no affinity with apparently ancestral forms elsewhere in the world.

Geological Succession.—The following time table of South American strata is modified from Scott.

Eras	*Periods and Epochs*	*Age*	*Occurrence*
Psychozoic	Recent or Post-Glacial		
Quaternary	Pleistocene (Glacial)	Pampean	Pampas of Argentina, also Equador Brazil, Chile, Bolivia Caverns of Brazil
Cenozoic (Tertiary)	Pliocene	Monte Hermoso Catamarca Parana	Extensive areas in Patagonia. Some extend into Tierra del Fuego
	Miocene	Santa Cruz Patagonian	
	Oligocene	Deseado (Pyrotherium beds) Astraponotus beds	
	Eocene Paleocene	Casa Mayor (Notostylops beds)	
Mesozoic	Cretaceous		

Scott summarizes the successive horizons as follows:

Paleocene. There are no marine Paleocene rocks, hence the inference is that the continent was largely emergent. Connection with Africa (Gondwanaland) may have continued into this epoch, but probably was severed during the Cretaceous. Hence the difficulty of deriving the South American mammals from known African orders, such as the Hyracoidea and Proboscidea, as some have argued.

There is evidence, although questionable, of the existence of the Antarctica-Australian bridge, which might account for the remarkable similarity between Australian and South American marsupials. The South Polar region could not have had so severe a climate as now, or passage across it, even were the land connec-

tions existent, would not have been possible. Communication with the Eurasian continent was probably roundabout, by way of North America.

Eocene. During the Eocene, North and South America were completely severed, apparently across Costa Rica-Panama, and there was apparently no connection with any other continent. Isolation was complete. Connection with Australia seems highly improbable, otherwise there would certainly be placental mammals in Australia derived from South America. Were such animals formerly existent they have utterly died out, leaving only the monotremes and marsupials. Usually when the two groups, placental and marsupial, are in competition, it is the marsupials that perish. Our knowledge of the relative organization of the two groups makes this the only understandable result.

During Eocene time the Andes were much lower than at present. Their great height in the south was probably attained not earlier than Pliocene time.

Oligocene. Paleogeographers believe that the Greater Antilles were broadly united into a common land mass known as Antillia, which existed during most of the Eocene but, due to great submergences during the late Eocene and Oligocene, was broken up into a chain of islands much smaller than the present Greater Antilles—Cuba, Haiti and Santo Domingo, Puerto Rico, etc. At all events, the Oligocene was for South America a time of complete isolation, so that it is difficult to be sure of the relative age of the Deseado formation, for instance (see table), as direct comparison with the Oligocene mammals of North America or Eurasia cannot be made, there being no forms in common.

Miocene. During the Pliocene, connection with North America was reëstablished, but, as we have seen, migrations of terrestrial animals followed slowly, for more than mere closing of a water barrier is necessary; hence the fauna of the Santa Cruz formation in the far south is still entirely a native evolution, with no known immigrant phase, such as appeared in the Pliocene. This, together with the marvellous abundance and perfection of the fossils, many of which are those of animals apparently buried alive in wind-borne volcanic ash, makes the study of the Santa Cruz fauna one of the most interesting and profitable of all. Matthew says that the reunion is dated from the appearance of *Megalonyx* in the Lower Pliocene of North America.

The Patagonian stage is marine, as the region was submerged beneath a shallow epicontinental sea. The finding of Cetacea (whales) in the Patagonian strata comparable to those in the Maryland Miocene establishes not only the geologic age of the former but also the fact that no land-bridge with Africa could possibly have existed at this time or the whales could not have intermigrated, as they surely did.

After the retreat of the Patagonian sea the Santa Cruz beds, which we have mentioned, were laid down, in part river deposits but largely the air-borne volcanic ash which preserved the entombed specimens with such great perfection.

While immigrants from North America may already have entered South America, none had as yet reached far Patagonia, whence the Santa Cruz animals come. Known fossil plants of Miocene time indicate luxuriant tropical forests comparable to those alive today in Brazil and Bolivia. The Santa Cruz animals come from too far south and too high an altitude for such plants to live in, and hence there is no direct record of their botanic surroundings at all. The mild climate which is indicated points to open plains with occasional trees, as in the African veldt.

Pliocene. With the ushering in of Pliocene time the climate becomes cooler, and this increases as time goes on until the austere conditions of the Pleistocene Glacial period are reached. The latter was never so severe as in the northern hemisphere, however. The paths of intermigration were now fully open to traffic, with all that that implies, and now for the first time appears the van of the increasing tide of immigration from north to south and from south to north. Climatic barriers, ever more prohibitive of north and south movement than of east and west, must to a certain extent have prevailed, for there never is such freedom of interchange of animals as between the Old World and the New.

A large portion of Patagonia was encroached upon by the seas, which extended in places to the Andes, while the broad valley of the Rio de la Plata was a gulf. The continental deposits of the Pliocene are of Parana, Catamarca, and Monte Hermoso age, the last being the most recent.

Pleistocene. As we have seen, the ice-sheets were much less extensive than in the northern hemisphere, rather were they localized, due perhaps not so much to temperature as to general differences in elevation. The climate must have been drier, for there is

evidence of great dust storms, carrying immense quantities of air-borne material, thus producing the loess of the Pampas formation. This covers vast areas of Patagonia and Argentina and entombs thousands of animals of Pleistocene age, some of which seem to be comparatively recently extinct. The relative age of the Pampas formation is equivalent to the Sheridan or Equus beds of the north, so called from the abundance of fossil horse remains, and there is, as we shall see, evidence of greater freedom of faunal interchange between the two continents than ever before. On account of the more consolidated character of the Pampas deposits they seem of greater antiquity than do the Equus beds. Their approximate age, however, is attested by the contained fossils.

Another source of Pleistocene mammals is the limestone caverns of eastern Brazil. Here, while the perfection of preservation is not so great as in the Pampas, the numbers are much greater; in one instance no fewer than 500 opossum jaws having been recovered from half a cubic foot of cavern earth.

The Pleistocene witnessed the extinction of a greater part of the ancient South American stocks which for millions of years had multiplied and passed on to leave the land to their somewhat altered descendants. The same is true of the immigrant element, such as the true horses. Why, one may conjecture, but there is no demonstrable cause or causes. As in North America, horses reintroduced by man throve mightily, showing that the physical environment other than the critical climates of the Glacial period was hardly responsible. An instance will serve to emphasize this point. Horses were first landed in Buenos Aires in 1537; by 1580, only 43 years later, their feral descendants had spread west and south until they had reached the Straits of Magellan: a remarkable development in a human generation and a half, even if they had the aid of mankind in their dispersal.

The Fauna

In studying the mammals of South America two remarkable vistas are unveiled to us of such typical, and at the same time contrasting, character that it is well to concentrate on those, with only such mention of the other ages as may be necessary for our understanding of the emphasized two. They are the Santa Cruz Miocene, when the fauna was entirely indigenous, and the Pampas Pleistocene, when interchange with North America was fully

established and the fauna was mixed, partly indigenous out of the Santa Cruz stock and partly immigrant from North America.

The origin of the native South American fauna has been alluded to, partly North American or via North America from the Old World, partly Australian (if the reverse of this last statement is not true), and partly, although doubtfully perhaps, African. Add to this the probability that certain orders, notably the edentates, were a purely local development and, while derived from some one of the primitive mammalian world stocks, nevertheless had their inception and subsequent evolution in South America, where they were first found. To be sure, there are so-called Old World edentates, aard varks and pangolins, but the feeling is that they are convergent toward the New World representatives of the so-called order and that the *Edentata* of common usage is not a natural group in that the two divisions are not blood-related.

Santa Cruz Fauna

The South American radiation had already been under way for millions of years when the Santa Cruz Miocene phase was reached. Land connection with North America had not as yet been reëstablished, hence the faunal interchange could not have been effected between such remote areas as North America and far Patagonia. The Santa Cruz animals are still entirely indigenous; but it is almost the last age of which this is true, for by Catamarca time (Pliocene) the first immigrants appear in the form of certain true Carnivora. These have been identified as dogs, raccoons, and bears, but the material is so fragmentary that precise identification is not only difficult but open to question. However, these are the first scouts of the invading army; there seems to be no doubt of that.

Scott has entirely exhausted his adjectives applicable to the strange Santa Cruz animals. They are so unlike anything alive to-day that, with very few exceptions, one would look the living world over in vain for comparisons. As he says, "It is extremely difficult to convey to the reader any adequate conception of this great assemblage of mammals, because most of them belonged to orders which have altogether vanished from the earth and are only remotely like the forms with which we are familiar in the Northern Hemisphere. To one who knows only these northern animals, it seems like entering another world when he begins the

study of the Santa Cruz fossils." There are gaps in the history of these forms, due in part to accidents of collecting, some of which future exploration will certainly fill, and also to the fact that Miocene Patagonia had comparatively few trees, so that typically arboreal, or even forest-dwelling forms, like the primates and others which must have existed toward the tropics, are hardly represented at all.

One rather remarkable thing about the Santa Cruz mammals, which is at once apparent from the figure, is the very moderate size of the known forms; most of them were actually small, only one or two, such as *Astrapotherium*, being actually large as compared with a pointer dog which is taken as a standard of comparison.

Marsupials.—As we have seen, the true Carnivora have not yet arrived, yet every fauna has a certain balance, though not an equal one, between its plant- and flesh-eating forms, the latter being much the less numerous. This is due to the ease of obtaining plant food, whereas the carnivores not only feed upon the herbivores but each individual must necessarily destroy numbers of them in the course of a lifetime. It is only in the remarkable Rancho la Brea of Los Angeles that the reverse is seemingly true of terrestrial animals, for there the carnivores, cats and wolves, are by far the more numerous. This is due to the capture of the latter by the tar death trap when they came to prey upon the unfortunate herbivores that formed the lure, and does not represent the true ratios of the time among the uncaught.

In Santa Cruz time it is the marsupials that fill the rôle of carnivores. These sparrassodonts, as they are called, seem to have a rather close affinity with the living thylacine or Tasmanian wolf. (See Australian Adaptive Radiation, Chapter XVIII.) Three genera are sufficiently well known to characterize in full. There was a wolf-like form which, because of its similarity to *Thylacynus* and its earlier age, has been called *Prothylacynus* (see Fig. 241,9). The representatives of this genus equalled modern wolves in size and prowess, but, if one may judge from *Thylacynus*, were far inferior to them in shrewdness and intelligence and yet could hold their own in a fauna where no true wolves existed. That they fulfilled the rôle of wolves and were probably equally successful in their day is evident. Another interesting beast was *Borhyæna*, described as possessing a short cat-like head and looking not un-

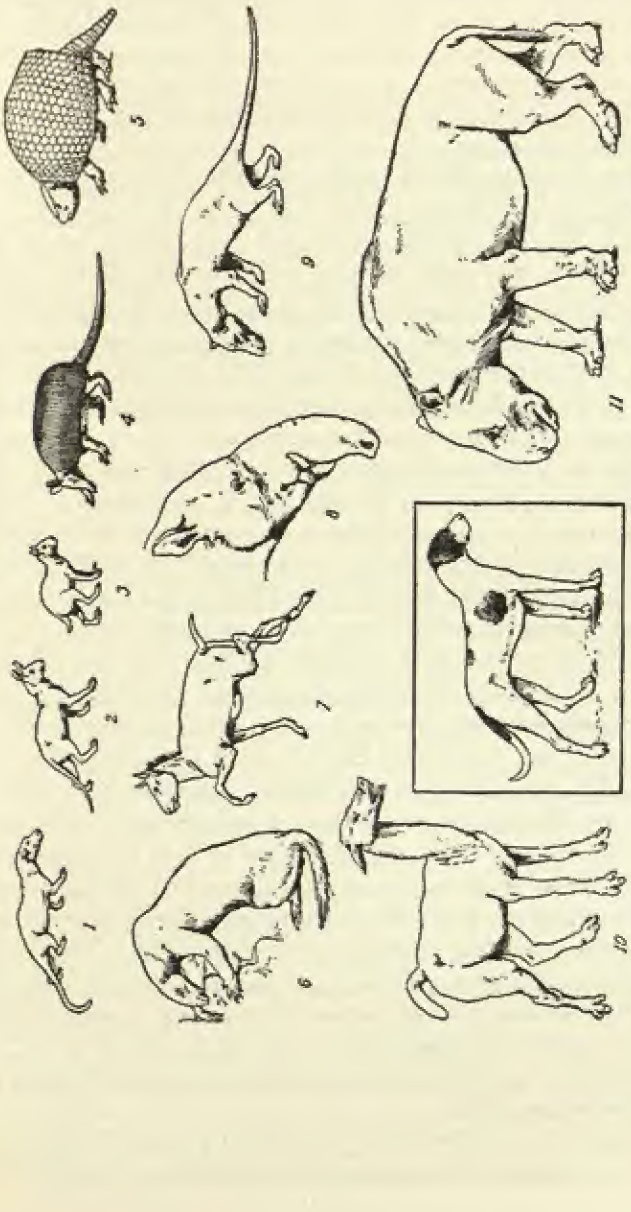

FIG. 241.—Representatives of the South American Santa Cruz fauna. 1, *Cladosictis*; 2, *Protypotherium*; 3, *Eocardia*; 4, *Stegotherium*; 5, *Propalaeohoplophorus*; 6, *Hapalops*; 7, *Thoatherium*; 8, *Astrapotherium*; 9, *Prothylacynus*; 10, *Theosodon*; 11, *Nesodon*. Drawn to the same scale as the modern pointer dog within the rectangle. (After Scott.)

like a small puma. His rôle was probably that of the larger modern cats. The rôle of the lesser beasts of prey, like the badgers and minks, was filled by *Cladosictis* (see Fig. 241,1) and its allies. Opossums were common, although more like the Australian phalangers perhaps than the common Virginia opossum of America. The latter must, however, be a survivor of the same general race. These forms maintained the balance of nature as the types used for comparison do to-day.

Rodents.—Of the herbivorous animals the first to be mentioned are the rodents (see *Eocardia*, Fig. 241,3), which varied in an extraordinary manner. As genera they are all extinct, although doubtless more or less akin and presumably comparable to their living descendants. Tree porcupines, chinchillas, cavies (guinea pig), coypus, and such forms, arboreal, cursorial, possibly aquatic, constitute this element of the fauna. (The Canadian or tree porcupine of North America is a surviving descendant of these old-time forms which has emigrated northward.)

Edentates are perhaps the most characteristic feature of the neotropical region. They vary greatly within the group but have certain characters in common, some of which are remarkably primitive, others high specializations. Linnæus' old order Bruta (Edentata) included both Old and New World forms characterized among other things by the deficiency of their teeth, although not all are toothless, as the word edentate implies. The New World forms have remarkably complex articulations between the successive vertebræ as compared with the relatively simple ones of the Old World, so that authorities have divided the order into the Xenarthra (Gr. ξένος, strange and ἄρθρον, joint), or New World edentates, and the Normarthra, or Old World aard varks and pangolins. As we have seen, the inclusion of two such different types in the same order may be an unnatural one. At all events there is no evidence of genetic relationship. The Xenarthra of Santa Cruz time included armadillos characterized by a bony body armor. These animals are present in the fauna of to-day, but it is doubtful whether many of the known Santa Cruz genera can be considered ancestral to those now in existence. Such a one as *Stegotherium* (see Fig. 241,4) was probably fossorial in habits, as are the modern armadillos.

Glyptodonts were another very remarkable group of edentates, also heavily armored, but, unlike the armadillos in which the

carapace consisted of a variable number of movably articulated rings, they had a box-like shell composed of rosettes of fused polygonal plates. They also bore a head shield, as well as one protecting the tail. They were rather conservative forms, varying largely in tail armor. In Santa Cruz time the glyptodonts were comparatively small, two feet or less, although one characteristic genus, *Propalæohoplophorus* (Fig. 241,5), made up for it in length of name, but that was a posthumous happening for which nature was not responsible. As Scott says, "their carapace departed less from the armadillo type than that of their gigantic descendants."

Sloths (*Tardigrada*). We know nothing of the Miocene tree sloths, but this is evidently due in large part to the character of the Santa Cruz environment, and not to the fact that they did not exist. It is possible that exploration further to the north, in the tropical forests of Brazil, would reveal these as well as a far greater abundance of monkeys and armadillos which are the actual ancestors of the existing forms. It is probable, however, that fossils will not be found, for it is as a rule in semi-arid or desert regions that the paleontologist finds his material, never in a tropical forest, except by the luckiest chance.

Ground sloths (*Gravigrada*) were leaf-eating and therefore required trees or shrubs as a food source, but not necessarily forests, if they frequented them at all. Hence the Santa Cruz environment was greatly to their liking, and their numbers and variety are amazing. As compared with their Pleistocene descendants they were small, none exceeding a black bear in size, and many were no larger than foxes. The head was small, the body long with a heavy tail and thick-set limbs, especially the hinder pair. They had long hook-like claws for uprooting and pulling down the branches of trees, and this necessitated walking on the outside of the hind foot, on the knuckles in front. Apparently they were covered with long coarse hair, at least their Pleistocene descendants were in two remarkably preserved instances, and they sometimes possessed vestiges of armor in the form of scattered dermal ossicles buried in the skin. Enamelless teeth were present in the rear of the jaws, while in front they used the toothless horny skin of the mouth, gathering their food as do the ruminants with a long prehensile tongue. Among the Santa Cruz ground sloths were probably the direct ancestors of the later giant sloths. *Hapalops* (see Fig. 241,6) is a representative Santa Cruz genus.

Ungulates.—To most of the hoofed animals the group name of Notoungulata has been given to stress their aloofness from the ungulates of the rest of the world. For it must be remembered that relative ease of intermigration makes the hoofed animals of Arctogæa, which includes roughly the northern land masses plus Africa, more or less akin, and all decidedly familiar to us, whereas Notogæa, or South America, placed its peculiar stamp on the native ungulates within its borders.

There are four suborders of Notoungulates, all out of the same ancestral stock, whatever that may have been, condylarth or hyracoid. Of these the first to be mentioned are the *Toxodontia* (*i. e.,* bow tooth in allusion to the sharp curvature of the grinding teeth). These were the most numerous in individuals of any of the ungulates, heavily and clumsily built and having but three toes fore and aft—feet hardly adequate, apparently, to the creature's weight. They ranged up to a modern tapir in size and were occasionally horned, the horns being odd in number of course to correspond to their odd-toed feet, for that and the reverse correlation generally hold, although with some remarkable exceptions. *Nesodon* (see Fig. 241, 11) is the largest of the Santa Cruz toxodonts and seems to have been the lineal ancestor of the Pleistocene *Toxodon* itself, the last of the line. There is reason to suppose that their habitats were partially aquatic, like those of the hippopotomi, and the feeding habits may have been comparable, although in the toxodonts the teeth were longer crowned and fitted for a harsher herbage.

The *Typotheria* (see Fig. 241,2) were anomalous creatures which, while closely related to the toxodonts, were vastly more rodent-like in general appearance. In size they were rarely, if ever, larger than a fox. Two most characteristic genera are *Pachyrukhos,* not larger than the rabbit which it must have resembled, at least superficially. It had long-crowned teeth. *Hegetotherium,* another form, was considerably larger and was a long-enduring genus, its racial life extending into the Pliocene.

Entelonychia. Every now and then there has appeared an anomalous group which, while clearly of ungulate affinities, departed widely from the conventional in the character of the feet. Such were the Ancylopoda or chalicotheres, first known from the Miocene of Europe and Asia and later from North America. The American representative is *Moropus* (*i. e.* sloth-foot, clawed

like those of the sloths), known by many complete skeletons from the famous Agate Spring Quarry of western Nebraska, one of which is mounted at Yale. This creature, while suggestive of the rhinoceroses in many details of teeth and structure and of the horses in its general proportions, departed from both in having laterally compressed and deeply cleft unguals which must have been sheathed in rather powerful claws instead of hoofs. The chalicotheres are looked upon as aberrant perissodactyls.

Nature has repeated the same experiment in the Entelonychia, taking this time the toxodont stock and developing grotesque creatures, long of limb and small of head, fully as remarkable and powerful as the chalicotheres. The latter were clumsy, especially in the fore limbs, which lacked the mobility of those of the ground sloths, for instance. Hence they could hardly have been used for pulling down the branches of trees to obtain the tender twigs and leaves which formed the staple food of the sloths. Dr. Matthew has suggested that they may have been used by *Moropus* in digging for water in an arid land. This may well be but would hardly suffice as a *reason* for the evolution of such curious structures, for many African ungulates—zebras and antelope—dig for water with perfectly normal hoofs. It may be that in the several clawed ungulates the claws were used for digging, but rather to loosen the earth around the roots of the trees, which could then be borne down by the straddling animal until the foliage could be reached. At all events, the Entelonychia were convergent toward the chalicotheres and may well have had a comparable manner of life, whatever it may have been, which influenced the trend of evolution in the one group as it did in the other. As in *Moropus*, the Entelonychia were large animals, in each instance exceeding greatly the bulk of their associates. They equalled a large ox or rhinoceros in size, although *Moropus* at least was much taller.

The *Astrapotheria* were ill known, as the fossils are generally very imperfect. There is a remarkable variation of size within the group, for they ranged from one extreme to the other as among Santa Cruz animals. The high-crowned head and large tusks, together with evidence of a well-developed proboscis, make these animals the most elephant-like of Santa Cruz forms. They differ, however, in that the tusks are *canine* teeth, whereas in the true Proboscidea they are incisors. Furthermore, there are no other Santa Cruz ungulates which have canine tusks, so that in this the

astrapotheres are unique (see Fig. 241,8). Scott says of them further, "Their limbs were long and not very massive, the feet short, five-toed and somewhat elephantine. They form an isolated group, traceable to the most ancient mammal-bearing beds of South America. Their relationships are obscure and more complete material is needed to solve the problem of their origin." Both the Entelonychia and Astrapotheria became extinct shortly after Santa Cruz time, whereas many of the notoungulates carried on until the Pleistocene.

Yet another order was the *Litopterna*, which were in many ways among the most interesting of all, chiefly, perhaps, because of their remarkable convergence toward the true horses on the one hand and the camels (llamas) on the other. Hence the members of this group would probably look less strange to us than any of the indigenous South American ungulates. The Litopterna also trace their separate lineage back to the earliest Tertiary stages. Thus they were a long-lived race. By Miocene time they had differentiated into two very distinct families, the Macrauchenidæ or llama-like forms, and the Proterotheriidæ or pseudo-horses which converged in a most remarkable manner toward the true equines.

These animals agreed with the perissodactyls in having odd-toed feet, the digits numbering either three or one in both fore and hind feet. The tarsus, on the other hand, was more suggestive of the artiodactyls, and the wrist is distinctive in its serially arranged bones, comparable in arrangement to the Condylarthra, such as *Phenacodus* (see Fig. 170), a curious admixture of the characters of different orders of mammals.

The Macrauchenidæ included the strange *Theosodon* (see Fig. 241,10), apparently the direct ancestor of *Macrauchenia* of the Pleistocene. It looked not unlike a modern llama, except for its three-toed feet. Its teeth also differed in being curiously pointed in the front of the mouth, which must have given the animal a strange reptile-like look when the mouth was open or the lips drawn back.

The proterotheres, or pseudo-horses, Scott says, were almost the only Santa Cruz animals which would not appear grotesque. As restored they are graceful little creatures, somewhat deer-like of body but again of course with odd-toed feet, three-toed in *Proterotherium* and *Diadiaphorus* and but one-toed in *Thoatherium* (see

(Fig. 241,7). Thus *Diadiaphorus* converged toward *Merychippus* or *Hipparion* among true horses and *Thoatherium* toward *Equus*. In *Thoatherium*, however, the digital reduction had gone even farther than in the modern horse, for the vestiges of digits two and four were reduced to tiny nodules, whereas in *Equus* they are long splints reaching more than half the length of the cannon-bone.

The proterotheres, unlike the macrauchenids, did not survive the Pliocene, for they were termini of a long evolutionary line, no trace of which has been found in the younger rocks.

Pleistocene (Pampas) Fauna

Another great vista of South American life is seen in the Pleistocene, where in the widespread Pampas formation there has been found a wonderfully rich fauna, although again composed of creatures of the open country and of temperate climate. Some, the indigenous element, are the direct descendants and therefore the culmination of several of the evolutionary lines which were represented in the Santa Cruz. Others were immigrants from the northern hemisphere which, as is generally the case with an invading army, were living on the country and giving the natives a severe competition, which may have been one reason for the almost total extinction of the latter. As we shall see, very few and insignificant have been their survivals after millions of years of existence.

Of the indigenous creatures of the Pampas the most conspicuous were the few surviving notoungulates and the edentates. It is interesting to note that, while some of the latter followed up the line of migration (although in the reverse direction from the invading hordes) and actually established themselves in North America, the ungulates did not and may never have been found outside the limits of Neogæa.

Of the *notoungulates* the typotheres are represented by *Typotherium*, itself the last of its race, a creature of moderate size and with chisel-shaped front teeth. *Toxodon* (see Fig. 242,5) likewise represents the terminal member of its phylum and, like its Santa Cruz forebear *Nesodon*, was probably semi-aquatic in its habits, a huge creature with small three-toed feet and with continually growing, sharply curved grinding teeth.

Macrauchenia (see Fig. 242,3) is again a last survivor, this time of the Litopterna. It was somewhat like its ancestor *Theosodon* but much larger, and the recession of the nasal bones, together

with certain depressions about the bony nostrils, is looked upon as evidence for the existence of a very well-developed proboscis, similar but longer perhaps than in the modern tapirs. Both neck and legs were very long, and its three-toed feet were stout and well fitted to bear its weight. The teeth have curious pit-like cavities on their grinding surface. Altogether *Macrauchenia* must have been a ludicrous animal, an efficient browser but one which could not survive the competition of the new arrivals from the north, nor perhaps the environmental changes of the Glacial period, although the present-day conditions might suit it very well.

The *edentates* reach their climax of specialization, although the species were apparently much fewer than during Santa Cruz times.

Tree sloths and anteaters, existing survivors of the order, were doubtless present further to the north, but their actual remains are very scanty, possibly through accident of preserval. Armadillos, also survivors to the present, were very many, some of them largely exceeding the existing ones in size.

Ground sloths were huge, vastly greater than any of their forebears. There were three families: (1) Megalonychidæ, although *Megalonyx* itself, which gives its name to the family, is recorded only from North America. (2) Mylodontidæ, represented by *Mylodon* (see Fig. 242,7), which is both North and South American and is next in size, a ponderous brute with dermal ossicles imbedded in the skin. There are preserved in the British Museum specimens of the related genus, *Grypotherium*, found in a cavern at Last Hope Inlet, Patagonia, almost unique in the degree of preservation in that not only were the broken bones found still bearing the shrivelled remains of sinews and flesh, but large portions of the hide as well, apparently from one individual with ossicles and dense coarse tawny hair. These give evidence of having been cut from the animal by stone knives wielded by prehistoric man. Moreover, the presence of the creature's dung, consisting of entire grass and of masses of cut grass, together with human bones, stone implements, and remains of fire, seems to imply that it and possibly other individuals were actually held in captivity by man himself and finally used as food. If so, this implies one of two things: either the great antiquity of contemporaneous man in South America, or the comparatively recent extinction of *Grypotherium*. It is said that human artifacts have also been found associated with *Toxodon* of which we have spoken, and this oc-

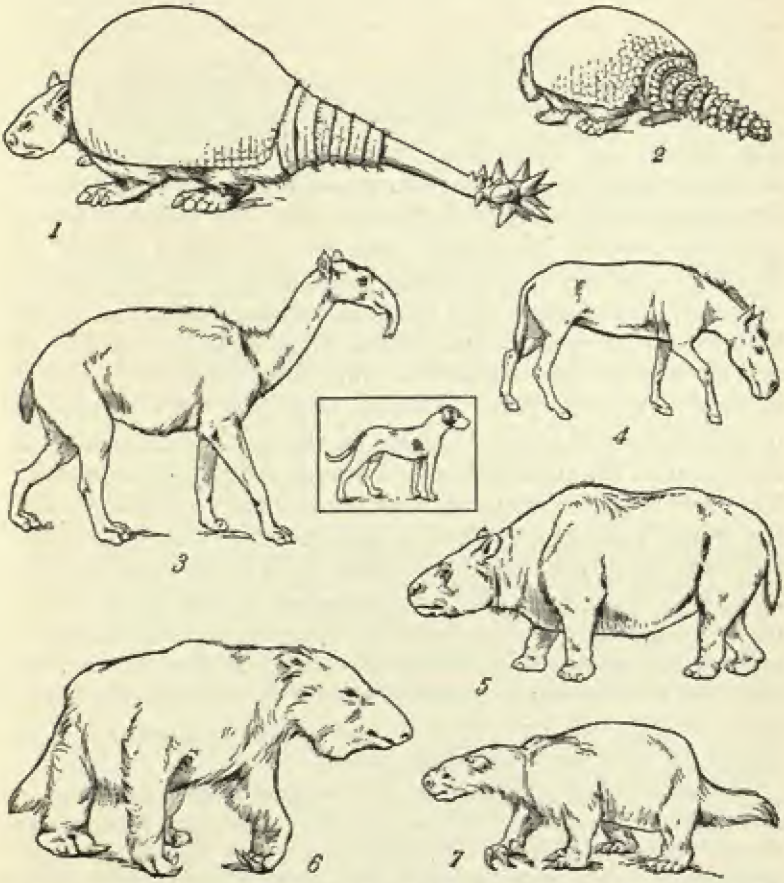

FIG. 242.—Representatives of the South American Pampas fauna. 1, *Dœdicurus*; 2, *Glyptodon*; 3, *Macrauchenia*; 4, *Hippidium*; 5, *Toxodon*; 6, *Megatherium*; 7, *Mylodon*. Drawn to the same scale as the modern pointer dog within the rectangle. (After Scott.)

currence, if true, is open to similar interpretation. The comparative freshness of the *Grypotherium* hide, together with evidence of the only other comparable case, that of the ground sloth *Nothrotherium*, found in New Mexico and now in the Yale Peabody Museum (see page 376), points to the theory of very recent extinction as the more probable.

The third family, Megatheriidæ, which includes *Nothrotherium* just mentioned, has as its representative genus *Megatherium* (see Fig. 242,6), first fully described by Sir Richard Owen. This creature was as large as an elephant, although not so tall, had a long spout-like symphysis of the lower jaw, and probably a long prehensile tongue. The family possessed no dermal ossicles for defense, as the size of its members probably gave them immunity to attack by any other than the great saber-tooth cat, *Smilodon*, and he may rarely have destroyed an adult animal. *Megatherium* and the smaller *Nothrotherium* are both known from North as well as South America. These creatures were both very ponderous of hind limbs and tail and walked on the extreme outer edge of the foot, with the long claws turned inward and clear of the ground. The fore limbs were relatively much more slender and mobile, and the animal must have walked on the knuckles of the hand with the claws bent back against the palm. It is quite apparent that they could rear on the hind legs, supported by the heavy tail as on a tripod, and use the fore limbs freely to pull down the branches of trees for the leaves, on which they normally fed. In the Yale specimen the hair which is preserved over the hip is long, coarse, rather brittle, and pale yellow in color. The living animal, however, may have been somewhat darker.

The armored glyptodonts of the Pampas were huge, with a carapace varying up to six feet, so that the entire animal sometimes reached twice that in over-all length, ten times the size of those of the Santa Cruz. The feet and legs were short and massive, with broad hoofs unlike the claws of the other edentates. There was comparatively little variation among the several species other than in the armor of the tail, which in *Dædicurus* (see Fig. 242,1) was a most remarkable structure, like the battle mace of a mediæval knight. These ultimate glyptodonts converged in a most amazing way toward the ancient armored dinosaur *Ankylosaurus* (see p. 485) of the late Cretaceous, resembling the latter in carapace-like armor, head shield, and battle-mace-like tail, and in all prob-

ability in immunity to attack except perhaps when very young. These late glyptodonts are also recently extinct, so that their shells, which once dotted the Pampas, are said to have been used by the Indians as huts or hogans in which to live. Few of the glyptodonts reached North America, as they were not particularly mobile types. They have been found, however, as far north as the Panhandle of Texas.

Primates were the typical ones found in South America to-day, such as *Cebus*, *Callithrix*, and others. Here again the fossil record does not give a complete story, as the center of their profusion was farther to the north in the tropical forests of which we have no record.

Marsupials are represented largely by opossums from the Brazilian caves, as the old predatory thylacines had gone. The latter cannot endure competition with wolves and foxes, the forerunners of which made their appearance in the Pliocene. A comparable case is found in the existing *Thylacynus* itself, which is now confined to Tasmania but whose remains are found in the superficial deposits of the Australian mainland, where it is now entirely extinct. Here the competitor was apparently the dingo dog, *Canis dingo*, the record of whose coming is lost in the obscurity of time, although it is generally believed to have been brought from Asia by the human aborigines, as it is closely related to the Indian dhole and could hardly have made the overseas migration unaided. The Australian Blackfellows, whose ancestors might have brought it over, are closest of kin to the Veddas of India, which sums the evidence.

Immigrant Fauna.—We have spoken of some of the South American animals which reached the northern hemisphere, edentates, rodents (Canada porcupine), and the like. The more virile North American forms, however, invaded South America in relatively greater numbers and gradually replaced many of the indigenous forms. The great extinctions of the Glacial period were ruthless for invaders and natives alike, few surviving into modern times. The Pleistocene ground sloths and glyptodonts, the notoungulates and the invading antelopes, horses, and mastodons have all been destroyed, not only in South America but, with the exception of the antelopes and horses, in the other continents as well. The immigrants did not all arrive at once but rather in successive waves of migration, the carnivores first.

Of the *Carnivores* all were of the ordinary North American types, with certain local peculiarities among those known from the Pampas. Of bears the short-faced *Arctotherium* is the only one known, but others, like those now living in the Andean highlands, may have existed. Of the cats the most interesting is the great saber-tooth, *Smilodon* (see Fig. 180), found also in North America and apparently the only enemy of sufficient prowess and armament to have attacked the ground sloths and mastodons. In fact the general belief is that their evolution was in a measure a response to such prey and that they could not survive the extinction of the latter, having reached an evolutionary *cul de sac* (see Chapter XXXIII). There were other large cats in the Pampas as well, true biting cats or Felinæ, allied to the living jaguar and puma, and smaller ones comparable to the ocelot.

The dogs were of at least three principal kinds: the bush dog, *Icticyon;* fox-like wolves, *Cerdocyon*, nearly related to those living to-day, and one, apparently *Cyon*, resembling closely the dhole of India. There were also raccoons, one very large one, and skunks and others, giving thus a comparatively well-rounded group of beasts of prey.

Ungulates. The Notoungulata, as we have seen, were relatively few and were but the last survivors of at least three of the old suborders, their place being taken by representatives of three orders of northern forms. Of the perissodactyls, there were true horses, *Equus* and the curious *Hippidion* (see Fig, 242,4), with two or three allied genera. There were also tapirs, which were the only perissodactyls to survive until modern times, although their range is much more restricted today. Artiodactyls include the llamas or camel-like forms, of which the wild guanaco and vicuña, with their domesticated derivatives, survive; deer and antelopes, the last being now extinct; peccaries, the only living American swine. Proboscideans of the genus *Dibelodon* (see Fig. 210) are also present, mastodons with rather complex grinding teeth and no lower tusks but with well-developed upper ones, each with a spiral band of enamel. These suffered extinction along with the northern mastodons. Why the true elephants, which were so well represented in the northern continent, together with *Mastodon* itself, never penetrated South America is a mystery.[1]

[1] A true elephant from French Guiana has been mentioned by Lartet (see Chap. XXXV).

This briefly summarizes the South American faunas and their evolution. Out of more primitive stocks there evolved strange and remarkable beasts, which probably were actually stranger in appearance than our restorations seem to show, for these are perhaps unconsciously influenced by the artist's knowledge of existing creatures, without which the reconstructions would be impossible. During the long period of isolation these throve in their various ways, adapting themselves admirably to the environmental needs, both physical and biotic. Some lines died out naturally, others flourished until they came into competition with the invading hordes and then perished, yet others actually stemmed the tide of northern invaders, crossed the land-bridge in the face of their numbers, and established themselves in the northern hemisphere, but never beyond the limits of the New World. The present-day survivors are very few. Among the edentates are armadillos, sloths, and anteaters; among the marsupials, opossums and *Cænolestes;* and among the rodents, tree porcupines, cavies, the chinchilla, and the capybara; and that is about all, only a remnant of a great and remarkable host.

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CHAPTER XXXIX

THE EVOLUTION OF MAN: ONTOGENY AND MORPHOLOGY

Man's Place in Nature

We have come to the culmination of our course and approach the high estate of man, the loftiest pinnacle of the evolutionary fabric, but one to which all of the laws governing the survival of the other creatures have nevertheless applied. In our research we cannot consider man, that is, physical man, as a being apart from his fellows of the animal kingdom; but whatever our prejudices, we must look the facts in the face and consider him merely as one, perhaps a very special one, among the great hosts of animal life. As in the case of the other creatures whose evolutionary history we have endeavored to understand, so with man we must enquire into his place in nature, learning what his nearest relatives are and whence and why he came.

Man a Vertebrate.—A brief diagnosis of a vertebrate mentions a number of characteristics such as the notochord, hollow, dorsally situated nerve-cord, perforated pharynx, and the like, all of which without exception are possessed by man the individual during some period of his career just as surely as by the horse, the dinosaur, the amphibian, or the fish. The evidence of man's vertebrate inclusion is therefore unquestionable.

Man a Primate.—Of the several classes into which the vertebrates are divided, man shares with the horse, the elephant, and even the saber-tooth the several characteristics—hair, warm blood, midrif or diaphragm separating the chest and abdominal cavities, young born alive and nourished by mammary glands—which make them mammals. He cannot therefore be debarred from that group any more than the others. Within the class Mammalia he is excluded from the egg-laying monotremes and the pouch-bearing marsupials, and included with those whose unborn young are nourished by the placenta (see Fig. 140); he is therefore a placental mammal. And of the four cohorts of Placentalia he is by a process of elimination narrowed down to the nailed arboreal forms, or

Primates, for he can be neither a clawed unguiculate, nor a hoofed ungulate, nor a finned cetacean.

Primates in General.—This name was given to the group by Linnæus, who wished thereby to emphasize the headship of the animal kingdom, the first in the sense of the highest. The word has, however, a deeper significance than this, for the primates are also among the first of the placental mammals in their antiquity and primitiveness. Along their chosen line of specialization, the feet, the horses and camels are, it is true, vastly further advanced than are the primates, and the same thing can be said of tooth modification in elephant and *Smilodon*. It is only in the brain and such correlated modifications as mental development entails that the primates may justly lay claim to superiority, for in other respects they are as humble and generalized a group, with very few exceptions, as the mammalian class contains.

Primates may be defined as nearly all arboreal, with prehensile limbs, having a more or less opposable pollex (thumb) and hallux (great toe). The five digits usually terminate in flattened nails, rarely claws; there is a clavicle, the orbit is completely surrounded by bone, the stomach simple, and the mammary glands are nearly always thoracic.

Classification of Primates

The classification of the primates has of course been subjected to the same vicissitudes as those of other orders, especially when fossil forms are found which link together apparently isolated living groups. An admirable study of primate interrelationships is that of W. K. Gregory (1916), from whom the following classification, somewhat abridged, is taken:

- Order Primates
  - Suborder Lemuroidea (lemurs or "half-apes").
  - Suborder Anthropoidea (monkeys, apes, and man).
    - Series Platyrrhini (New World monkeys).
      - Family Hapalidæ (marmosets).
      - Family Cebidæ (capuchins, howler monkeys, spider monkeys, etc.).
    - Series Catarrhini (Old World monkeys and apes).
      - Family Cercopithecidæ (monkeys, baboons, macaques, etc.).
      - Family Simiidæ (man-like or anthropoid apes).
      - Family Hominidæ (men).

Lemuroidea.—The lemurs (Figs. 243, 244) are the most ancient of living primates and as such have departed least from the ordinary quadruped. They are, however, exclusively arboreal, mostly nocturnal, and of comparatively low organization, which is manifest not only in their body but also in the brain, for the fore brain is relatively small and smooth and does not completely cover the hind brain as in the higher primates. The second digit of the foot bears a claw, the rest terminate in nails.

The present home of the lemurs is, above all, Madagascar, of which they are so highly typical that they constitute perhaps one-half of the total mammalian fauna. Lemurs are also distributed

FIG. 243.—Lemur, the aye aye, *Chiromys madagascariensis*, living, Madagascar. (After Owen, from Wortman.)

through the tropical forests of Africa and the Oriental realm. They are found fossil in the Eocene rocks of North America and of Europe. Two interesting relic animals belonging to this group still survive—*Chiromys*, the aye aye (Fig. 243), now living in Madagascar but having near allies among the long-departed fossil forms of North America; and *Tarsius*, the tarsier (Fig. 244), now confined to Sumatra, Borneo, Celebes, Java, and the Philippines, but which also had relatives in the American Eocene.

Anthropoidea.—The anthropoids are the most highly organized of primates, with 32 to 36 teeth, a completely closed orbit, two pectoral mammæ, feet usually prehensile and generally the hands also, pollex sometimes vestigial, and cerebral hemispheres richly convoluted, covering the cerebellum. This suborder includes all

primates other than the lemurs and this of course means man as well as the monkeys and apes. It is divided into two sharply marked series, the Old and New World primates, and these, so far as our evidence goes, represent parallel evolutions which, because of the long period of South American isolation (see page 622), must have diverged from a common ancestry in early Eocene time.

The Platyrrhini may be distinguished by the broad nasal septum (hence the name, Gr. πλατύς, broad, and ῥίς, nose); the thumb

Fig. 244.—The tarsier, *Tarsius spectrum*, living, East Indies and Philippines. (After Brehm.)

is not opposable, and sometimes reduced; the tail may be prehensile; there are no cheek-pouches nor ischial callosities. The family *Hapalidæ*, the marmosets or squirrel-monkeys, are small monkeys with a long, hairy, non-prehensile tail. The pollex is elongated, but the hallux very small. The latter bears a flat nail, while all of the other digits are armed with curved and pointed claws. These creatures are no larger than squirrels and are active forms, living among the trees in small groups. Their food consists of fruit, to which eggs and insects are added, a very common dietary.

The *Cebidæ*, the common South American monkeys, differ from the marmosets in the possession of an additional molar tooth in each jaw, making thirty-six teeth all told, in having flat nails instead of claws, and frequently a prehensile tail. These forms, none of which is as large as the larger Old World monkeys, are ex-

FIG. 245.—New World ape, the spider monkey, *Ateles pentadactylus*, living, northern South America. Notice the extremely reduced thumb and the prehensile tail. (After Brehm.)

clusively confined to the tropical forests, notably those of Brazil. Among the more remarkable are the slender spider-monkeys (*Ateles*, Fig. 245) whose prehensile tail is an organ of the greatest use; the howler monkeys (*Mycetes*), whose prodigious voice arises from an especially modified vocal apparatus; and the capuchins (*Cebus*), whose pathetic figures, garbed with human habiliments, are so often seen with itinerant musicians.

The group Catarrhini includes all of the Old World apes and man, excluding of course the lemurs. They are characterized by the possession of a narrow nasal septum with the approximated nostrils directed downward, thirty-two teeth as in man, and a non-prehensile tail, which may, however, be vestigial or entirely absent. The hallux, except in man, is fully opposable and the pollex as well, although often less developed.

The *Cercopithecidæ* are the monkeys and baboons, exclusive of the man-like apes, from which they differ in the fore-and-aft elongation of the molar teeth, the presence of ischial callosities on the rump, occasional cheek-pouches, a narrow breast-bone, and in the absence of the vermiform appendix. The baboons (*Cynocephalus*) are almost the only primates with the exception of man which have forsaken the arboreal for a terrestrial mode of life; but unlike man this has not resulted in an erect posture but a typically quadrupedal one. Their head is more dog- than ape-like, hence the generic name (Gr. *κύων*, dog, and *κεφαλή*, head), with powerful jaws bearing immense canine teeth which, added to the equally powerful hands, enable competition with the terrestrial creatures to be readily met. The old male mandrills (Pl. XXVI) are remarkable for their ferocity. These creatures are colored most gorgeously on the cheeks and ischial callosities, but colors which in themselves are beautiful—blue, scarlet, lilac—are in combinations which seem grievously misplaced. Thus while the fur is often beautiful and the colors lovely, the general effect is such that, as Cuvier says, "Il serait difficile de se figurer un être plus hideux que le mandrill." The mandrills, which are typical baboons, like the rest of their race, appear to be somewhat indiscriminate eaters, feeding upon fruit, roots, reptiles, insects, scorpions, etc., and inhabit open rocky ground rather than forests. Their present range includes Africa and Arabia.

Of the baboons Ditmars says: "It is fortunate for general animal life that their tendency to develop size and massive frame stopped where it did. If they had reached the size of the anthropoid apes, they would be among the most frightful creatures the earth has ever known."

The macaques are rather stoutly built monkeys, the tail being variously developed. They are both arboreal and terrestrial in habit but their principal interest lies in the fact that, whereas almost all are Asiatic, extending as far as Japan, one species, the so-

called Barbary ape (*Macacus inuus*) is North African and is the only living primate other than man which is found within the confines of Europe, as it has spread from northern Africa to Gibraltar.

Semnopithecus is another characteristic genus, containing very long-tailed, slender forms, short-muzzled, without cheek-pouches, and typical of a subfamily, the Semnopithecinæ. This group is both African and Oriental in its distribution.

The man-like or anthropoid apes, family *Simiidæ*, lay greatest claim to our interest, since they of all creatures come nearest to mankind, not only in similarity of structure, but in actual relationship, for they are our next of kin in that they and humanity spring without question from the same bough of the tree of life, and though the relationship is very remote according to human standards of consanguinity, from the evolutionary point of view it is very close. This does not mean that man arose from any known ape, or that any ape could ever in the course of evolution give rise to a man, but that man and the ape had at some not very remote time, geologically speaking, a common ancestor. It is, however, highly probable that were we to see this common progenitor in the flesh we would be at a loss for a descriptive term to apply to it if we excluded the word ape. The primates which we have discussed play a subordinate part, in that they serve to link man with the lower animals; the Simiidæ, on the other hand, are all-important, for only by an understanding of them and their habits can we come to a true appreciation of our immediate prehuman progenitors.

The Simiidæ are thus diagnosed: Man-like apes, tailless; no cheek-pouches or ischial callosities, except in the gibbon; arms much longer than the legs, an opposable pollex, a broad sternum, a vermiform appendix. Several extinct genera of Simiidæ are known, while among the living there are four: *Hylobates*, the gibbon; *Simia*, the orang; "*Anthropopithecus*" or *Pan*, the chimpanzee; and *Gorilla*, the gorilla. Of these the first two are Oriental, the last two African in their present distribution, although all are apparently Asiatic in origin (see page 673).

The gibbons (Pl. XXVII) are the smallest of the man-like apes, rarely exceeding 3 feet in height, but have relatively the longest arms, for the hands reach the ground when the creature stands erect. Ischial callosities are present—true of none of their allies—and they are variously colored. The jaws and dentition as in all

Simiidæ are adapted to a frugivorous diet, but the molar teeth are more primitive than in their relatives, although the upper canines are enlarged and saber-like, either for defense or, more probably, as a dietary adaptation. The skull is rounded, lacking the high sagittal crest[1] for muscle attachment seen in the adult males of the other genera, and the head is posed upon the vertebral column more like that of a man, doubtless a response to the erect posture which the ape assumes both at rest and in motion. This upright pose may have originated in connection with a change in the mode of locomotion. The primitive lemurs ran and jumped on the upper side of the branches, and hence were quadrupedal, whereas the gibbons swing beneath the branches, the arms being held above the head. "This acrobatic mode of locomotion, which has been appropriately called 'brachiation' (Lat. *brachium*, arm) by Professor Keith, very probably took rise in the earliest anthropoids and has been carried to an extreme specialization in the excessively long-armed gibbon. Thus the habit of sitting upright, which first set free the hands for prehensile purposes . . . very probably preceded the habit of brachiation and the loss of the tail, as it has also in the genus *Indris* among the lemurs" (Gregory). Huxley's description of the gibbons contains the following:

They "are true mountaineers, loving the slopes and edges of the hills, though they rarely ascend beyond the limit of the fig-trees. All day long they haunt the tops of the tall trees; and though toward evening they descend in small troops to the open ground, no sooner do they spy a man than they dart up the hill-sides, and disappear in the darker valleys." The voice is prodigious, much more powerful than that of any singer, and yet the animal has hardly half the height of a man and far less proportionate bulk. They walk erect with the arms either down, touching the knuckles to the ground, or above the head. The gait is quick, waddling, with no elasticity of step, and they are soon run down.

In the trees, however, their locomotive powers are quite another matter, as their method of progression is by brachiation, the hands and arms being the sole organs of locomotion, clearing spaces of

[1] The sagittal crest is a thin vertical ridge of bone running along the mid-line of the skull, the purpose of which is to give greater area for the origin of the muscles concerned in mastication than is afforded by the brain-case alone. The development of this crest implies increased jaw power over those forms which do not possess it; it is also more apt to be developed where the brain-case itself is small as in the creodonts.

12 to 18 feet with the greatest ease and uninterruptedly, for hours together. According to Duvaucel, they can clear 40 feet, which may be readily believed. They start and stop instantly with no appreciable slowing down or acceleration of speed. Moreover, their leaps not only require great strength, but the nicest precision. The significance of this mode of progression cannot be ignored, because of its educative value to the creature concerned, for every time such a hand leap is undertaken it requires the instantaneous solution of a mathematical problem, since an accurate estimate of distance, trajectory, direction, and the ability of the objective branch or branches to bear the impact of the creature's weight must all be estimated, and upon the correct solution of this problem depends the amount of muscular force to be used in order that the creature may neither under- nor overshoot the mark, and the penalty placed upon the incorrect solution of the problem and its practical application may be death! Nature has abundant opportunity, therefore, for the weeding out of the unfit and she places a high premium upon mental preparedness, more perhaps in the gibbon and other brachiating primates than in any other group of animals, and this undoubtedly was also true of the arboreal ancestors of man.

Osborn thus summarizes: "The gibbon is the most primitive of living apes in its skull and dentition, but the most specialized in the length of its arms and its other extreme adaptations to arboreal life. As in the other anthropoids, the face is abbreviated, the narial region is narrow, *i. e.*, catarrhine, and the brain-case is widened, but the top of the skull is smooth, and the forehead lacks the prominent ridges above the orbits; thus the profile of the skull of the gibbon is more human than that of the other anthropoid apes. When on the ground the gibbon walks erect and is thus afforded the free use of its arms and independent movements of its fingers. In the brain there is a striking development of the centers of sight, touch, and hearing [see diagram, Fig. 249]. It is these characteristics of the modern gibbon which preserve with relatively slight changes the type of the original ancestor of man."

The orang, *Simia satyrus* (Pl. XXVIII), the second of the oriental apes, is confined to the swampy, coastal forests of Sumatra and Borneo. It is reddish in color and rarely exceeds four feet in height, but, unlike the gibbon, it is very bulky, measuring two-thirds of its height in circumference. The arms are immensely long, the crea-

ture spreading from 7 feet 2 inches to 7 feet 6 inches. The head is short, round, and of great vertical diameter, with very closely approximated orbits. The skulls of the old males show a sagittal crest and the face is surrounded with a remarkable flaring rim of flesh which gives it a very ferocious aspect. The jaw is deep and massive, and the canines are very efficient either for the opening of fruits or for fighting. The principal weapons, however, when used against other animals, are the hands.

The great size of this ape renders it less agile than the gibbon and while highly intelligent it is sluggish in disposition, reposing with the back curved and head bowed until hunger stimulates it to activity. By day the orangs climb from one tree top to another and they descend to the ground only at night. They climb slowly and carefully, more like a man than an ape, and are nest-building in that they break off branches and lay them in a convenient crotch of a tree, thus forming a sort of platform whereon they repose, utilizing one nest until the food in the immediate vicinity is exhausted, when they move on and build another. These nests are 10 to 25 feet above ground. On the ground the orang runs laboriously and shakily on all fours and is soon overtaken by man. It never stands erect. "Dyaks tell of old orangs which have lost all their teeth, but which find it so difficult to climb that they maintain themselves on windfalls and juicy herbage" (Huxley). Normally the food consists of figs, blossoms, and young leaves, never living animals. The intelligence is very great, the hearing acute, but the vision less so.

The chimpanzee, *Pan pygmæus* or *Anthropopithecus troglodytes* (Pl. XXIX), is the first of the African apes and may readily be distinguished from the orang by its black hair, although the skin of the face and ears is apt to be light in color. In size they never exceed 5 feet but are not so bulky relatively as the orangs, and as a consequence are much more expert as climbers, swinging from tree to tree with great agility as do the gibbons. They rest in the sitting posture and sometimes stand or walk on the hind limbs, but run on all fours. The head of the chimpanzee is larger than that of the orang and the brow-ridges above and outside of the orbits are especially prominent. There is a sagittal crest for muscular attachment in the males. The brow-ridges and the prognathous or forward sloping teeth and receding chin strongly resemble those of the more ancient species of prehistoric man (see page 683).

In their nest-building the chimpanzees resemble the orangs; in their activity and biting propensities, the gibbons. There may also be more than one species as with the latter. They are confined today to west and central equatorial Africa, from Sierra Leone to the Congo. Chimpanzees are abundant.

Gorilla gorilla, by far the most formidable of the man-like apes, is also restricted to tropical Africa, extending from the Cameroon in the West across the Congo basin to Uganda and Tanganyika. There are apparently two species. A specimen killed in the Cameroon and now mounted in the museum of the Academy of Natural Sciences in Philadelphia stands 5 feet 1½ inches in height, and weighed in the flesh 418 pounds, while the Karisimbi male, shot by Akeley, measured 5 feet 7½ inches in height and weighed 360 pounds, the arm spread being 97 inches. The torso and upper limbs are immense, but the legs are short compared with those of man. If the latter were of human proportions the height would probably exceed 7 feet and the weight would approach 500 pounds. Even as it is one cannot but view this creature in terms of humanity, hence he becomes to the imagination one of the most terrible creatures upon earth, far more impressive than a much larger *quadruped* would be.

In describing the skull (see Fig. 247) Gregory says: "The gorilla carries to the logical extreme the frugivorous and fighting specializations which are foreshadowed in the chimpanzee. The head is lengthened by the forward growth of the muzzle and by the extreme backward growth of the skull-top. Thus the gorilla skull, to a certain extent, parallels that of the baboons. The supraorbital protrusion is now extreme. The . . . sagittal crest and widely flaring occipital crests attain an excessive development in old males, and are conditioned by the massive size of the muscles of the jaws and neck. The canines form great tusks and hence the muzzle and lower jaw are very wide in front. . . . Thus the fundamental resemblances to the human skull are largely disguised in the male gorilla, which is distinguished by the great tusks and massive cheek teeth, the divergent tooth rows, the baboon-like muzzle and protruding orbits, in contrast with the opposite specializations in man. The young female gorilla, on the other hand, except in the dentition, more distinctly approaches the human type than any other anthropoid."

The gorilla is the negro of the anthropoids, with the skin a dark

brown, approaching black, and coarse black hair which becomes gray with age. The limbs and body are markedly adapted to its gigantic and clumsy stature. It has departed from the primitive slender-limbed and arboreal type and exhibits a more or less transitional stage leading to ground-dwelling habits. As in the ground sloths, the long arms, stout, short legs, and widely expanded pelvis are adapted for the support of the enormous thorax and abdomen. The hands of the gorilla are more human than those of any other anthropoid, although the thumb is relatively smaller than in man and has not acquired the power of opposing itself to the other digits. So also the foot of the gorilla distinctly approaches the human type in several ways.

Carl Akeley, who collected material for the gorilla group in the American Museum of Natural History, gives us a picture of these huge apes which is in marked contrast with the popular conception based upon travellers' tales of their aggressive ferocity. He says: "I saw no indication that the gorilla is in the least aggressive or that he would fight even on just provocation. . . . The first gorilla I ever saw alive was a lone old male, who might be expected to show some war-like spirit, if that had been a characteristic of his tribe. I saw his face—ugly and wrinkled, but mild and gentle—across the valley and caught a glimpse of his gray back as he went over a log and up the slope through dense vegetation. . . . While I am certain that normally a gorilla is a perfectly amiable, good-natured creature who would not look for trouble, yet I am willing to concede that, in regions where he is more or less in competition with the natives and where he is constantly harassed in his efforts to fight hunger, an old male might occasionally become what might be called a 'bad gorilla'."

The gorilla is not a tree-dwelling animal. Only three were seen off the ground and these not more than ten feet up—no higher than a civilized boy would climb—and there was no indication that any of the other trees had been climbed. They never sleep in the trees but make their nests on the ground. They are not partial to fruits or nuts, preferring to feed on grass, herbage, and bamboo leaves. If they climb for food or at the approach of danger, they must come down the trunk they ascend, as they cannot swing from one tree to another. They always progress on all fours, as they are too bulky to walk on their relatively weak hind legs, and if they ever do so it must be with no more ease or grace

than a heavily built trained dog would exhibit in making a similar attempt. When they rise and beat their chests, it is not a challenge but an indication of curiosity (Akeley).

Hominidæ.—The family to which man belongs, the Hominidæ, bears the stamp of close relationship with the Simiidæ, the differences being mainly the direct outcome of terrestrial life, the assumption of the erect posture, and the development of the brain. The erect posture has coördinated with it the alternation in the curvatures of the spine, the more complete adaptation of the hind limbs to bear the weight of the body, the loss of the power of opposition of the great toe and its more complete development in the thumb, and the greater length of the hind as compared with the fore limbs.

"The anthropoids are chiefly frugivorous and typically arboreal; when upon the ground they run poorly and (except in the case of the gibbons) use the fore limbs in progressing. Thus they are confined to forested regions. Man, on the other hand, is omnivorous, entirely terrestrial, erect, bipedal and cursorial, an inhabitant primarily of open country. The anthropoids use their powerful canine tusks and more or less procumbent incisors for tearing open the tough rinds of large fruits and for fighting. Primitive man, on the contrary, uses his small canines and more erect incisors partly for tearing off the flesh of animals, which he has killed in the chase with weapons made and thrown or wielded by human hands. These implements and weapons also usually make it unnecessary for man to use his teeth in fighting and functionally they compensate for the reduced and more or less defective development of his dentition" (Gregory).

There is but one living genus, *Homo*, included within the family Hominidæ, and all existing men of whatever race or color are given but a single specific name, *sapiens* (*i. e.* to know). The divisions of this species into its various races, of which no fewer than 26 subspecies are recognized by Gregory, are, perhaps, unnecessary to our purpose, other than to enumerate the following:

Australian race: skull long (dolichocephalic); extremely prominent eyebrows; large teeth, especially the canines; tall, long-limbed; skin chocolate-brown; hair black, long and woolly. Habitat: Australia, Dekkan, Hindustan.

Negroid race: dolichocephalic, forehead round and childish, nasal bones flattened, teeth sloping (dental prognathism); skin

and eyes brown or black, hair the same color, short, woolly, not abundant. Habitat: Madagascar and Africa from the Sahara to the Cape of Good Hope.

Mongolian race: brachycephalic (short-headed), flat nose, small and oblique eyes; short and thick-set; golden-brown skin; sleek, coarse black hair; scanty beard. Dwell east of a line drawn from Lapland to Siam; Chinese, Tartars, Japanese, Malays, Eskimos, North and South Americans.

Caucasian race: A, Mediterranean, short, slender, long-headed, hair and eyes dark brown to black; B, Alpine, of medium height, stocky, round-headed, hair and eyes dark brown to black, eyes often hazel or gray in western Europe; C, Nordic, tall, long-headed, hair flaxen, red, light brown to chestnut, eyes blue, gray, or green. Habitat: Mainly Europe and North America; includes also Moors, Berbers, Egyptians, Kurds, Persians, Afghans, Hindus, Turks, Armenians, Africanders, and Australians (non-native, for natives see above).

Anatomical and Ontogenetic Evidences for Human Evolution

Anatomical Evidences

Limbs.—As with the elephant, man's body shows a number of primitive characteristics in addition to his specializations, the latter being developed within comparatively narrow limitations. The radius and ulna in contrast with those of the horse are both well developed and freely articulated so that the range of movement is ample, not only the hinge motion at wrist but the rotary one known as pronation as well. In the wrist the several bones are distinct, such as the scaphoid and lunar of the proximal row, which, in the Carnivora for instance, tend to coalesce into a single bone. The fibula of the lower leg is well developed and the foot has the primitive plantigrade position of the most archaic mammals.

The number of digits is unreduced from the primal five, nor are the phalanges either increased in number as in the whales or diminished, so that the primitive formula of 2, 3, 3, 3, 3 for the number of bones in both fingers and toes still prevails.

Skeleton.—The shoulder girdle yet retains the clavicle, linking the scapula with the sternum in contrast with all ungulates and

with the carnivores. The atlas which bears the skull, the sacrum or that portion of the vertebral column which lies between the hips, and the scapula or shoulder-blade all show certain reptilian characteristics.

Teeth.—The teeth are also primitive, short-crowned, of simple structure and pattern, bearing relatively few, low cusps. The two premolars which are present are simpler than the molars, all of which is in marked contrast with the forms we have studied—the horse, elephant, and camel.

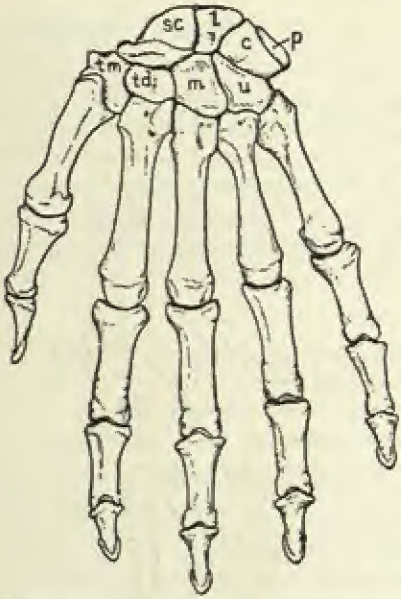

FIG. 246.—Human hand, *Homo sapiens.* Compare with that of *Phenacodus primaevus.* FIG. 170, B. *c*, cuneiform; *l*, lunar; *m*, magnum, *p*, pisiform; *sc*, scaphoid; *td*, trapezoid; *tm*, trapezium; *u*, unciform.

Soft Anatomy.—Man's soft anatomy also bears the mark of great antiquity, especially those organs having to do with his pre-natal nourishment (placenta). And the means whereby the intestine is attached within the body cavity, the mesenteries, have still the same arrangement seen in the quadrupeds.

Specializations.—These are, first, the erect posture, which has reacted upon the skeleton in several ways, for instance, the four *curvatures of the spinal column* which are reduced in number and degree in infancy and extreme old age. Second, the *basin-shaped pelvis* in contrast with the flattened form seen in the anthropoids. The form of the human pelvis aids in supporting the viscera while the body is in the erect position. The pelvis of human embryos is at first flattened, apelike, and only gradually assumes the basin form as they approach the time of birth. Third, *relatively short fore limbs*, the hands rarely extending below mid-thigh when the body is held erect. This shows the opposite extreme of a series as compared with the gibbon.

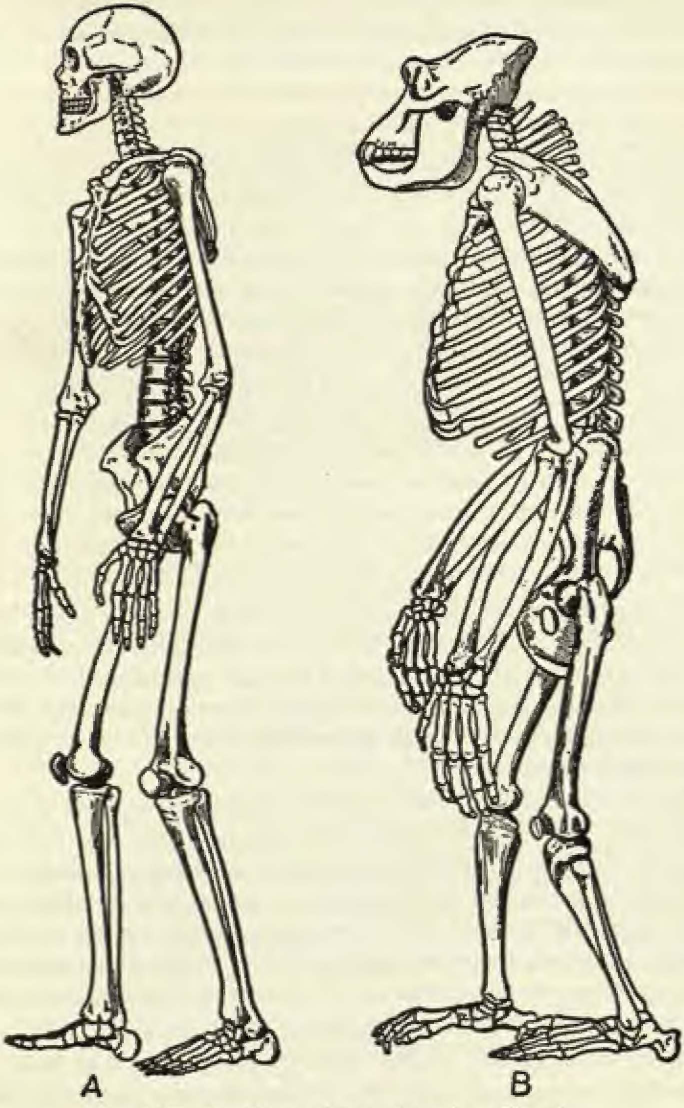

FIG. 247.—Skeletons of man (A) and gorilla (B).

With respect to *foot specialization*, in comparison with the foot of the anthropoid the human foot shows: loss of opposability of the great toe, occasionally offset in some primitive types of man; development of the shock-absorbing arch; tendency toward monodactyly, the axis of the foot running through digit one which thus becomes the "great toe," the others diminishing in size and length. In the fifth digit reduction in the number of phalanges is in progress as the distal ones tend to fuse in a certain percentage of human subjects.

Still another specialization is the *loss of hair* from the body, possibly as a result of the acquisition of artificial clothing. The evidence for this belief cited by Matthew (1915) follows: "(1) It is accompanied by an exceptional and progressive delicacy of skin, quite unsuited to travel in tropical forests. I do not know of any thin-haired or hairless tropical animal whose skin is not more or less thickened for protection against chafing, the attacks of insects, etc. (2) The loss [of hair] is most complete on the back and abdomen. The arms and the legs and, in the male, the chest, retain hair much more persistently. This is just what would naturally happen if the loss of hair were due to the wearing of clothes,—at first and for a long time, a skin thrown over the shoulders and tied around the waist. But if the loss of hair were conditioned by climate it should, as it invariably does among animals, disappear first on the under side of the body and the limbs and be retained longest on the back and shoulders." A high specialization is the loss of pigment in the skin of fairer races.

The normal human *dentition* contains the same number of teeth, thirty-two, as that of the other Catarrhini, so that the reduction from the original forty-four is a primate and not a human characteristic. The human teeth, however, are reduced in relative size as compared with those of the anthropoids, the canine no longer exceeds the other teeth in length and it is tending to become incisiform. There is also a loss of the diastemata or spaces between the teeth into which, in the ape, the opposite canines fit.

In the anthropoids the *movement of the lower jaw* is obliquely transverse, ruminant-like; in the human being it is in all directions and partly of a rotary character. This is correlated with the reduction of the interlocking canines. That tooth reduction in humanity is still progressing is shown by the fact that one of the premolars and the second incisors are often reduced and sometimes wanting,

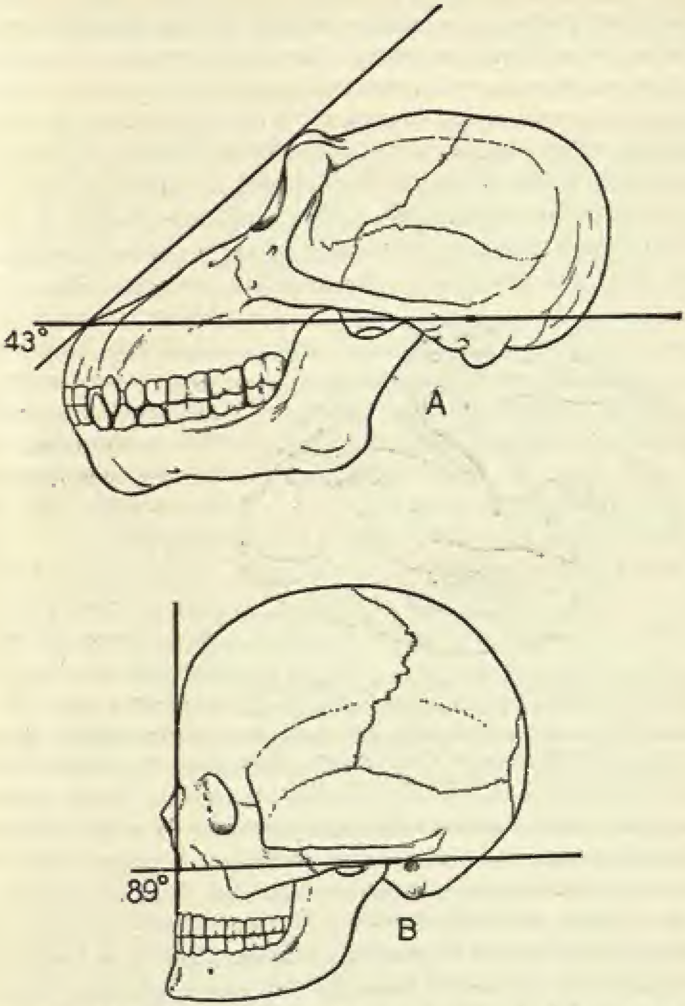

Fig. 248.—Facial angle of man (B) compared with that of chimpanzee (A). (Modified from Mivart.)

and the same is true although to a less extent of the third molars, the so-called wisdom teeth.

The tooth reduction is in turn correlated with the shortening of the muzzle and jaw symphysis—the facial portion of the skull, that concerned with the senses and appetite, in contrast with the enormous expansion and deepening of the brain-case, the seat of mentality. This change in the proportions of face to cranium is expressed in terms of the *facial angle* that is formed between two lines lying in the sagittal plane of the skull, one of which is drawn from the lower margin of the nasal aperture to the ear opening, the other from the forehead to the maxilla (see Fig. 248). In the higher races of mankind this facial angle approaches a right angle, averaging 85°; in the anthropoid, such as the chimpanzee, it is much less, not more than 45°.

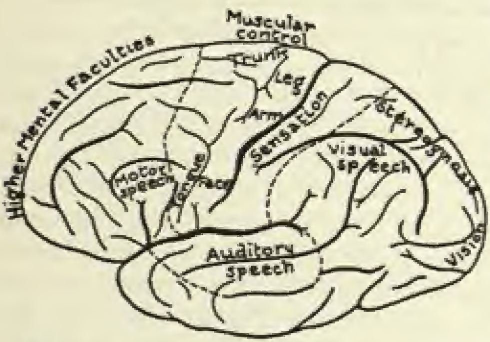

FIG. 249.—Side view of human brain, cerebrum, of high type, showing chief areas of muscular control and of sensory impressions of sight and hearing, also prefrontal area in which higher mental faculties are centered. (Modified from Starr.)

The human *brain* is one of nature's marvels, exceeded in actual size only by that of the elephants and of the greater whales. In relation to bodily weight, man's brain exceeds that of any other creature except some excessively small vertebrates such as the humming-birds and smaller mice. In these forms there has been a dwarfing as a result of evolution, as an increase or decrease in bulk physically seems to be more rapidly attained than a change in brain size in the same animal. Growth of body unaccompanied by equivalent brain growth was seen in the dinosaurs *Stegosaurus* and *Brontosaurus*.

Aside from its mere increase in size, the human brain (see Fig. 249) is also of the highest vertebrate type, the huge cerebrum entirely covering the cerebellum, so that the latter is invisible from above. Greater area of the external cortex, the so-called "gray matter" which is the real seat of intellect, is obtained by a deepening and further complication of the depressions between the

convolutions. And the great development of the frontal lobes, particularly, gives ample opportunity for the expansion of the higher intellectual faculties. In its subtle fineness of detail, in its ability to record and often to reproduce an almost infinite number of mental perceptions, and in all those other resident faculties which together make up the higher intellectual characteristics of humanity, the human brain stands preëminent as the most complex structure evolution has produced. But a comparison with the brain of an orang shows the self-same fundamental characteristics; the proportions differ, but in a broad way the shapes are similar and the major convolutions are alike, in other words, the two brains differ not in kind but in degree, and that of man is physically merely a relatively larger and more refined example of the same fundamental type. With regard to mental retrogression in the apes Beebe says: "Young orang-utans in their 'talk' as well as in their actions, are the counterparts of human infants. The scream of frantic rage when a banana is offered and jerked away, the wheedling tone when the animal wishes to be comforted on account of pain or bruise, and the sound of perfect contentment and happiness when petted by the keeper whom it learns to love,—all are almost indistinguishable from like utterances of a human child. But how pitiless is the inevitable change of the next few years! . . . Slowly but surely the ape loses all affection for those who take care of it. More and more morose and sullen it becomes until it reaches a stage of unchangeable ferocity and must be doomed to close confinement never again to be handled or caressed." Mr. Beebe adds to this observation in a letter as follows: "I find that while sexual maturity is attained at about six years, the females seem little affected and remain gentle and affectionate. The males, however, begin at about five years to become morose and sullen. This applies both to chimpanzees and orangs. These statements apply only to several animals which have attained their sexual majority in the [New York Zoölogical] Park and even among them there is great variation."

The final human characteristic which lifts man high above his fellow creatures is *articulate speech*, the means whereby communication, especially of higher abstract thoughts, is made primarily possible; for the development of a mature written language is clearly the outgrowth of antecedent speech. This human faculty has had great influence in the development of the higher mental traits.

Thus it will be seen that comparative anatomy shows very emphatically our fundamental resemblances to the other anthropoids and that if we would look for differences we must compare details of structure and development rather than distinctions of a larger sort. As Huxley truly said: "The structural differences between man and the man-like apes certainly justify our regarding him as constituting a family apart from them; though, inasmuch as he differs less from them than they do from other families of the same order there can be no justification for placing him in a distinct order. . . . Perhaps no order of mammals presents us with so extraordinary a series of gradations as this—leading us insensibly from the crown and summit of animal creation down to creatures, from which there is but a step, as it seems, to the lowest, smallest, and least intelligent of the placental Mammalia. It is as if nature herself had foreseen the arrogance of man, and with Roman severity had provided that his intellect, by its very triumphs, should call into prominence the slaves, admonishing the conqueror that he is but dust."

Vestigial Organs.—Drummond mentions no fewer than seventy such relics which he most appropriately calls the scaffolding left in the body, relics of old-time conditions and needs for which the modern human economy has no further use. They are veritable historical documents enclosed within the limits of each human frame during part or the whole of its existence and may be viewed in no other light. Certain of these features disappear with growth and maturity, others persist during the lifetime of their possessor.

One of these persistent vestigial features is the *direction of hair* on the body. That upon the arms, for instance, slopes from shoulder to elbow and from the wrist upward and outward in such a way that, were the hands clasped above the head with the elbows pointing downward, a posture said to be assumed by the orang, the hair thus arranged sheds the falling rain (see Plate XXVIII). In all anthropoids except the gibbon the same direction of hair prevails as with mankind, hence the conclusion of a bygone community of habit between man and these apes is irresistible. Then, too, the absence of hair on the terminal segments of the digits, its scarcity on the second, and greater abundance on the first are true of the anthropoids as well as of man.

The *vermiform appendix* (Fig. 250) has been mentioned as a diagnostic characteristic of the family Hominidæ and also of the Si-

miidæ. In man it is not only apparently useless but is sometimes a veritable deathtrap. With herbivorous mammals, on the other hand, its homologue, the cæcum, is large and of high digestive value. Even in man the appendix has the same structure as the large intestine—peritoneum, muscular coat, and mucous layer. In the embryo it has the same caliber as the rest of the bowel but soon ceases to grow and may actually be as long in the new-born babe as in the adult.

The *Darwinian point* to the ear is a little conical projection from the rolled or unrolled margin of the ear, more frequent in the male than in the female, as are all atavistic features. This is in man a

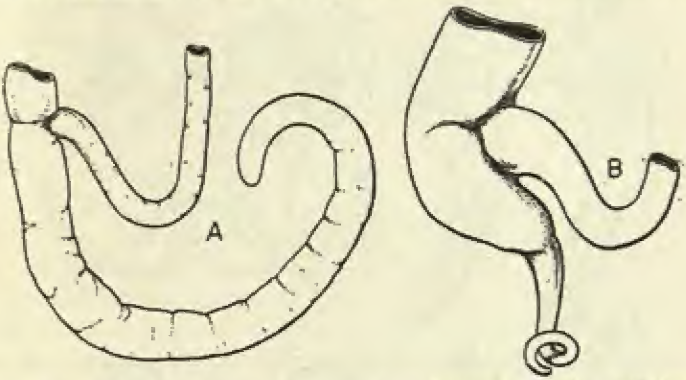

FIG. 250.—Cæcum of (A) kangaroo and vermiform appendix of (B) human embryo. (After Wiedersheim, from Jordan and Kellogg's *Evolution and Animal Life*, D. Appleton and Co.)

relic of the pointed ear found in the human embryo and in lower mammals and is, as Darwin says, a "surviving symbol of the stirring times and dangerous days of his animal youth."

Thin bands of *muscle*, formerly of value in moving the shell of the ear to aid in the appreciation of sound, are still present but usually functionless, as are also the present but involuntary hair-erecting muscles of the scalp. Most of the dermal muscles, in fact, so well developed in lower animals for twitching the skin, are retained in the human face only where they are used for the expression of the emotions. Doubtless their retention is in part of defensive significance as they may well have been used to strike terror into the breast of an opponent. In addition to this, they also aided in the expression of the emotions, as of pleasure or pain, and together with the voice formed the first elemental speech.

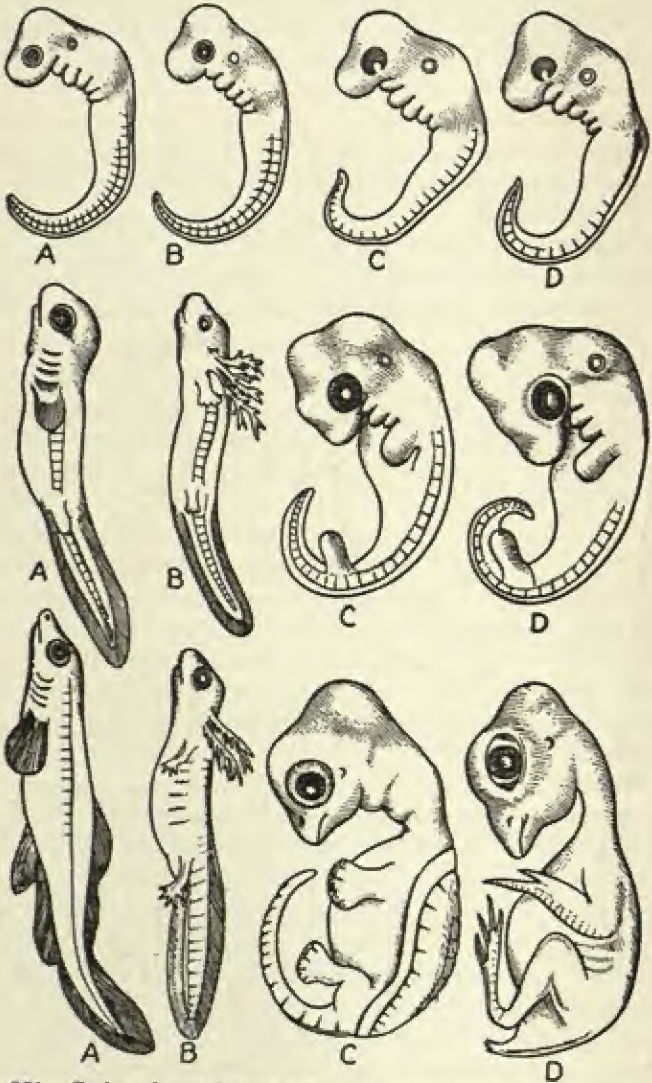

FIG. 251.—Series of vertebrate embryos at three comparable and progressive stages of development. A, fish; B, salamander; C, tortoise; D, chick. (Continued on next page.)

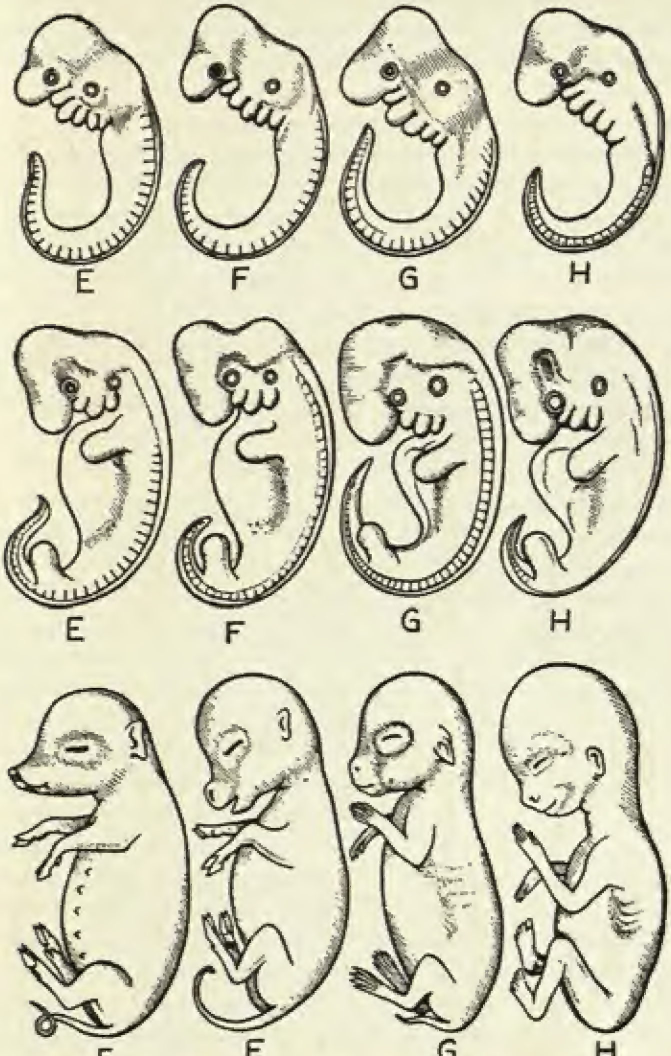

FIG. 251.—(cont.)—Series of vertebrate embryos. E, hog; F, calf; G, rabbit; H, Human. (After Haeckel, from Romanes' *Darwin and after Darwin*. Copyright, Open Court Publishing Co.)

A further vestige is the *plica semilunaris*, a crescentic fold of membrane in the inner corner of the eye which represents the very efficient third eyelid or nictitating membrane of the eyes of many mammals and of birds. In man it is relatively larger before than after birth. The *pineal body* of the brain is connected in reptiles, notably *Sphenodon*, with a third eye, really the first primordial vertebrate eye. In man this is present as a vestige deep hidden beneath the mass of the cerebrum.

In other mammals that portion of the upper jaw which bears the incisor teeth is separated off by a suture, and is known as the *premaxillary bone*. In man and the chimpanzee this suture is normally obsolete, yet the poet Goethe predicted that some day the separate premaxillary would be found in man, and so it has been. Moreover, the *frontal bone*, single in man, paired in the dog, is paired in an Abyssinian skull in the Yale collection.

Ontogenetic Evidences

Ontogenetic Vestiges.—Embryology teaches us much of the past life of any race and this is just as true of humanity as of any other created being; for the unfolding of the miniature man shows precisely the same one-celled condition of the ages-remote protozoan ancestry; the same cleavage stages, morula, blastula, and gastrula, as any other metazoan; the gradual assumption of chordate characteristics, of notochord, of hollow nervous system, of gill-clefts; the budding of limbs, at first as ill formed as those of the earliest slime-borne amphibian emergent from the old limiting aquatic environment; the perfected limbs and well-developed tail of an ancient placental mammal, and the ultimate loss of this and other embryonic structures, until a man is born into the world. Thus these wonderful changes, wrought in the dark, reproduce, as in a pageant, the historic changes brought about by the evolutionary process during the long night of the geologic past.

Certain of the ontogenetic features may be more specifically mentioned, such as the *gill-clefts*, of which there are four in the embryo. Occasionally certain of these communicate with the throat so that openings remain on the sides of the neck through which fluids taken in at the mouth can trickle, or white patches on the skin betray their former position. The first gill-cleft, the so-called spiracle of the fish, normally persists and forms the eustachian tube connecting the middle ear with the throat for the pur-

pose of equalizing the air-pressure on either side of the drum. The auricle in fact is developed from this first gill-cleft and the hearing organ may be subsequently repeated down the neck. As Drummond says: "In some human families, where the tendency to retain these special structures is strong, one member sometimes illustrates the abnormality by possessing the clefts alone, another has a cervical ear, while a third has both a cleft and a neck-ear—all of these, of course, in addition to the ordinary ears."

The *tail* is indicated in the human skeleton by the four or five bones at the lower terminus of the spine, coalesced in the adult into the coccygeal bone which is concealed beneath the flesh; but in the embryo not only is it present but is free, movable, and has muscles for wagging it! These are usually reduced later to mere ligaments but may permanently retain their muscular character. The external tail may also persist.

FIG. 252.—Russian "dog-man," Adrian Jeftichjew, showing atavistic development of hair. (After Wiedersheim.)

The *lanugo*, or clothing of dark hair which covers the entire body except the palms and soles at the sixth month of prenatal life, usually disappears before birth, but in rare circumstances may persist and give a permanently hairy aspect to both face and body. This fœtal hair is also found in other hairless mammals such as the elephants and whales, and can have but the one historical significance, harking back to the day when hair was a racial necessity and not a superfluity as it is to-day in all three groups.

The "awful grasp of a baby," as one has put it, is also significant, for the *power of grip*, notably great during the first few weeks of its life when it needs the most constant care, sensibly weakens later as experiments have shown. These consisted in the suspending from a stick or from the finger by the power of their hands alone

some sixty infants which were under a month old, and in at least half of these the experiment was tried within an hour of birth. "In every instance, with only two exceptions, the child was able to hang on to the finger or a small stick, three-quarters of an inch in diameter, by its hands . . . and sustain the whole weight of its body for at least ten seconds. In twelve cases, in infants under an hour old, half a minute passed before the grip relaxed, and in three or four nearly a minute. When about four days old . . . the strength had increased, and nearly all when tried at this age could sustain their weight for half a minute. About a fortnight or three weeks after birth the faculty appeared to have attained its maximum, for several at this period succeeded in hanging for over a minute and a half, two for just over two minutes, and one infant of three weeks old for two minutes thirty-five seconds. Invariably the thighs are bent nearly at right angles to the body, and in no case did the lower limbs hang down and take the attitude of the erect position. Furthermore, the child shows no sign of distress and no cry is uttered until the grasp begins to give way" (Drummond).

FIG. 253.—Human babe, three weeks old, supporting its own weight for over two minutes. Attitude of lower limbs and feet more simian than human. (From Romanes' *Darwin and after Darwin*. Copyright, Open Court Publishing Co.)

This is of course one of the many instances, mainly structural, however, which point to the old-time arboreal life, not perhaps that the infant of that day clung directly to the tree but that the mother did and had to have her hands free for brachiation, hence it was necessary for the infant to cling to her.

Another phenomenon which has received a similar interpretation—that of arboreal life—is the occasional *dreams* one has of falling through space with the violent instinctive effort often undergone to prevent disastrous consequences. And the strange thing about it is that in the dream the fall never ends fatally, for that is an experience which could not be transmitted to offspring, for such would not exist, while that of the fall could. Jack London in his book *Before Adam* makes much of this. Roosevelt says of nightmares, although without necessarily implying an his-

torical interpretation to them: "Civilized man now usually passes his life under conditions which eliminate the intensity of terror felt by his ancestors when death by violence was their normal end and threatened them during every hour of the day and night. It is only in nightmares that the average dweller in civilized countries undergoes the hideous horror which was the regular and frequent portion of his ages-vanished forefathers, and is still an every-day incident in the lives of most wild creatures" (*Scribner's Magazine*, May, 1910). But perhaps too much emphasis has been placed upon dreams.

These examples out of many—Wiedersheim says 180—are sufficient to show that the human body cannot be considered as a perfect final work of creation but rather the ultimate product of eons of evolutionary change, resulting in a very imperfect being from the physical point of view—a veritable museum of antiquities!

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CHAPTER XL

THE EVOLUTION OF MAN: PALEONTOLOGY

Paleontological Evidence of Human Evolution

Our evidences for human evolution thus far discussed are such as were derived from the existing; we have now to trace, in so far as we may, the actual evolutionary history of the primates and of man as derived largely from paleontological records.

Origin of Primates

Stock.—There is but little doubt that two important orders of modern mammals, the Carnivora and the Primates, had a common origin, diverging mainly along lines determined by a dietary contrast, as the former have become more strictly flesh-eating or predaceous, the latter largely vegetarian and more completely arboreal. Back of each group lie as annectant forms the Insectivora, not perhaps such as are alive to-day, as all these are specialized along diverse lines, but generalized insectivores possessing, because of their primitiveness, a wider range of potential adaptation. Matthew is "disposed to think of these, our distant ancestors, at the dawn of the Tertiary, as a sort of hybrid between a lemur and a mongoose, rather catholic in their tastes, living among and partly in the trees, with sharp nose, bright eyes and a shrewd little brain behind them, looking out, if you will, from a perch among the branches, upon a world that was to be singularly kind to them and their descendants." Thus we can define the stock as a relatively large-brained arboreal insectivore, comparable to the existing tree-shrews (*Ptilocercus*) of the Oriental realm, of primitive but adaptable dentition, and especially of progressive mentality.

Time.—The time of primate origin must have been not later than Paleocene, as primates, clearly definable as such, are found in the Lower Eocene rocks of both Europe and North America.

Place.—The simultaneous appearance of the primates in the Old World and the New gives rise to the same conclusions as to their place of origin and their migrations thence as with other modern-

ized mammals (see page 516). It suffices now to say that their ancestral home was Holarctica, probably within the limits of the present continent of Asia, whence they migrated southward along the three great continental radii (see map, Fig. 254). The impelling cause of this migration was the increasing northern cold, before which the northern limitations of the tropical forests retreated, carrying with them the primates which, in general, although with noted exceptions, are dependent upon such an environment for their sustenance.

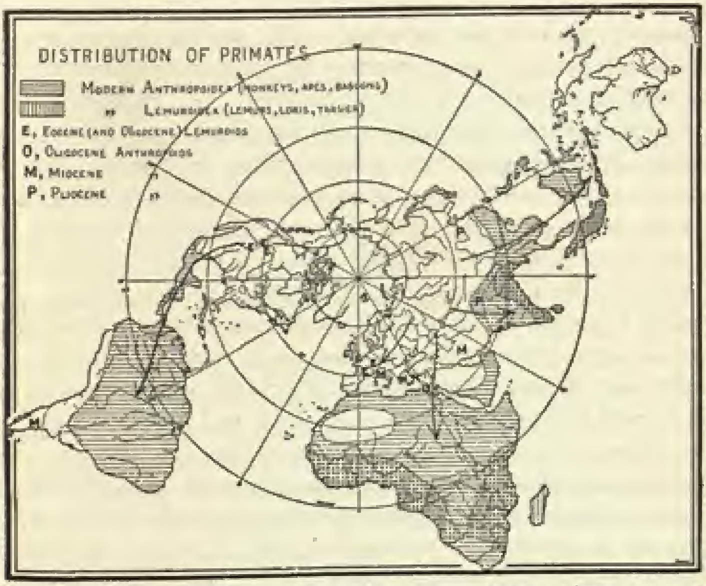

FIG. 254.—Map of primate distribution and probable migratory routes. (After Matthew. Courtesy of the Yale University Press.)

Geologic Record.—Primates are found in the North American sediments from Paleocene to late Eocene time, when they became extinct. Thus, while their remains constitute a relatively large percentage of the total fauna of the Eocene, primates are utterly unknown on this continent from that time until the coming of man. In Europe the record is similar except that the extinction occurred at a somewhat later date, the Oligocene. Furthermore, they reappear in Europe in the Lower Miocene, their second European extinction being in the Upper Pliocene shortly before the first appearance of mankind.

But in southern Asia, Africa, and South America the evolution of primates seems to have been continuous since the first great southward migration. The evidence, however, is not so much the historical documents as the presence of primates in those places at the present time; the fossil record is not entirely lacking although highly incomplete. The South American monkeys may have had their origin in the ancient North American primates, or more doubtfully, the stock may have come by way of Africa.

Origin of Man

Summary of Primate Evolution.—The paleontological record, after the most critical study checked by comparative anatomy and other related sciences, appears as follows: "In Palæocene time, some sixty million years ago, there lived arboreal insectivores, relatives of the existing tree shrews, while in Eocene time are found the ancient relatives of lemuroids and tarsioids. The Lower Oligocene rocks of Egypt have given us two jaws of supreme importance, one, *Parapithecus*, being annectant in character between the tarsioids and anthropoids, the other, *Propliopithecus*, representing a form leading to the gibbons and perhaps to the higher apes and man. From India and Europe in rocks of Miocene and Pliocene age comes *Dryopithecus*, of which several species are known from fragmentary jaws and teeth and a single humerus. These appear to be closely related both to the existing great apes and man and probably represent the common ancestral stage" (Gregory). While *Dryopithecus* is very incompletely known, nevertheless we are fairly safe in assuming that it was a big-brained, arboreal, brachiating primate, and that it links the ancestry of man most closely with the chimpanzee-gorilla group, in spite of wide differences of habits and adaptation of the present-day descendants.

Place.—Evidences point to central Asia as the place of the descent from the trees of the human precursor, the reasons for this belief being several. First, it was central for migrations elsewhere; Europe, on the other hand, where much of the most conclusive and perfect evidence for fossil man is found, is too small an area for the divergent evolution of the several human species. Second, Asia is contiguous to the oldest known human remains, which were found in Java and in China. Third, it was the seat of the oldest civilizations, not only of the existing nations which, like

the Chinese, trace their recorded history back to a hoary antiquity, but of nations which preceded them by thousands of years, and whose records have not yet come to light. This antiquity vastly exceeds that of the nations of Europe or of the Americas or of Africa. Fourth, central Asia is the source of almost all of our domestic animals, many of which have been subjected to human will and control for thousands of years, and this is equally true of many of our domestic plants. This is not due to the fact that man first reached civilization in Asia, but rather that he chose for his companions the highest and best of their several evolutionary lines, and Asia was the place of all others upon earth where the evolution in general of organic life reached its highest development in late Cenozoic time. Fifth, climatic conditions in Asia in the Miocene or early Pliocene were such as to compel the descent of the prehuman ancestor from the trees, a step which was absolutely essential to further human development.

Impelling Cause.—We look for a geologic cause back of this most momentous crisis in the evolution of humanity, and we find it in continental elevation and consequent increasing aridity of climate, especially to the northward of the Himalayas. With this increased aridity and tempering of tropical heat came the dwindling of the forested areas suitable to primate occupancy. Barrell has suggested that this diminution left residual forests comparable to the diminishing lakes and ponds of the Devonian, which upon final desiccation compelled their denizens to become terrestrial or perish. The dwindling of the residual forests would have an effect upon the tree-dwellers which may be expressed in precisely the same words. Once upon the ground the effect upon even a conservative type—and the primates in general, where constant conditions prevail, are slow of change—would be the rapid acquisition of such adaptations as were necessary to insure survival under the new conditions, for mankind is progressive, with a prolonged childhood and retarded maturity of the skull, hence a greater brain and increasing ability to change from the forests to open country and severer conditions. The great apes, on the other hand, are conservative, with early growth and maturity and with inability to change with changing conditions, hence they migrated along their own kind of environment to their present distribution where tropical forests continue to be available and as a consequence retained their arboreal life and with it a stagnation of progress.

The result has been, at any rate on the part of the three larger apes, a partial degeneracy from the estate of their common ancestry with mankind; the gibbons seem to have deteriorated less, while terrestrial man has risen to the summit of primate evolution.

Time.—The time of the descent cannot have been later than early Pliocene and was probably not earlier than Miocene time; when the terrestrial ape-man became what we would call human was perhaps later, but certainly during the Pliocene, which makes the age of man as such measurable in terms of hundreds of thousands of years!

Significance of the Descent from Trees.—As a result of the descent from the trees, certain definite factors were called into play, each of which had its effect on the further evolution. Briefly enumerated, these are: (1) assumption of erect progression; (2) liberation of the hands from their ancient locomotor function to become organs of the mind; (3) loss of the easily obtainable food of the tropical forests, necessitating the search for sustenance, both plant and animal, and man became a hunter; (4) need of clothing with increasing inclemency of the weather, especially during the long winters; (5) freedom from climatic restrictions—when an omnivorous diet and clothing and the use of fire were acquired man was no longer limited to one definite habitat and the result was dispersal; (6) the development of communal life, rendered possible by the terrestrial habitat. Primates are at best gregarious, submitting, as in the gorilla, to the leadership of the strongest male, but it is only by communal life with its attendant division of labor that man can rise above the level of utter savagery.

Evolutionary Changes.—Human evolutionary changes which are recorded are:

More erect posture
Shorter arms
Perfection of thumb opposability
Reduction of muzzle and of size of teeth
Loss of jaw power
Development of chin prominence
Increase in skull capacity
Diminution of brow-ridges
Diminution in strength of zygomatic or temporal arch
Increase in size and complexity of brain, especially frontal lobes
Development of articulate speech

Fossil Man

Fossil remains of man are found under two conditions, in river valley deposits and in limestone caverns which served first as a dwelling-place and later as a sepulcher. Of these the caverns have been by far the most productive, but they contain only the remains of the later races, as the caverns probably did not become available for human occupancy before middle Pleistocene time, the Peking locality being an exception.

The rarity of human fossils may be explained, first, by the various burial customs, which seldom are sufficiently perfect to preclude the possibility of alternate wetting and drying or of rapid oxidation, both prohibitive of fossilization. If man lived and died in the forests, the chances for his fossilization, in common with other forest creatures, were very remote, for the remains of such are almost invariably destroyed by other animals, by dampness, or by fungi, and rarely attain a natural burial in sediment. If, on the other hand, he dwelt in the open, the chances of so shrewd a creature being caught in the flood waters and thus buried in sediment were not very great. However we account for it, the fact remains that relics of ancient man are rare and are valued accordingly.

In North America.—Repeated instances of seemingly ancient man have been brought to light in North America, such as the "Calaveras skull" of the California gold-bearing gravels, which was satirized by Bret Harte; the Nebraska "Loess man"; and those of the Trenton gravels: none of which, with the possible exception of the last mentioned, has proved to be really old in the geologic sense. Indirect evidence of human antiquity, that is, the association of North American man with animals which are now extinct, while very rare has been reported in at least two or three highly authentic instances. The first of these at Attica, New York, was attested by Doctor John M. Clarke, then New York state geologist. Four feet below the surface of the ground, in a black muck, he found the bones of the mastodon (*Mastodon americanus*), and 12 inches below this, in undisturbed clay, pieces of pottery and thirty fragments of charcoal. The charcoal may have been of natural origin, but the presence of the pottery seems conclusive. The other instance was that of the remains of a herd of extinct bison (*Bison antiquus*) found near Smoky Hill River,

Logan County, Kansas, and thus described by Professor Williston: An "arrowhead was found underneath the right scapula of the largest skeleton, embedded in the matrix, but touching the bone itself. The skeleton was lying upon the right side. . . . The bone bed when cleared off . . . contained the skeletons of five or six adult animals, and two or three younger ones, together with a fœtal skeleton within the pelvis of one of the adult skeletons. The animals had evidently all perished together, during the winter. There was no possibility of the accidental intrusion of the arrowhead in the place where found. . . . It must have been within the body of the animal at the time of death, or have been lying on the surface beneath its body."

Further instances of the same association—arrow or lance points and bison remains—are reported from a point near the southeastern end of the Staked Plains of Texas. The artifacts are of beautiful workmanship, and of them the following emphatic statement is made: "They are certainly and positively contemporaneous with that fossil bison and the associated fauna of mammoths, camels, and extinct horses—of a type found elsewhere in beds of known Pleistocene age" (Cook, 1925).

What is claimed to be another genuine case of such an association, this time of the actual human bones, has been reported from Florida. This find, which has been described by Sellards, was made at Vero, eastern Florida, in 1913. The fossil human bones are from two incomplete skeletons and are found in strata which also contain remains of the following extinct species: *Elephas jeffersoni*, *Equus leidyi*, a fox, a deer, the ground sloth *Megalonyx jeffersoni*, and the American mastodon.

In South America.—A number of finds have been recorded from South America, notably by the late Florentino Ameghino of Buenos Aires, who contributed so largely to our knowledge of South American prehistoric life. An expert from Washington, Doctor Aleš Hrdlička, has, however, studied with the utmost care the locality and character of each of these finds in the western world, and has expressed the opinion that none is of an antiquity greater than that of the pre-Columbian Indians.

Further evidence along the same line lies in the uniformity of type, except for minor distinctions, of all native American peoples. There is no such racial differentiation as that seen in the Old World, and the argument is that there has not been time for such a deploy-

ment. The area and conditions as an adaptive radiation center are surely ample.

In Africa.—The only African relics thus far reported are of prehistoric cultures, comparable to those of southern Europe, in certain caverns of the Barbary States. There has also been reported from Oldoway ravine, in what was formerly German East Africa, a human skeleton of undoubted antiquity. It is described, however, as being neither a very early nor a primitive type. A very remarkable African type came to light in 1921 at Broken Hill Mine in Northern Rhodesia, where, at the extreme depth of a natural tunnel 120 feet long, portions of two individuals were found, one being the skull of *Homo rhodesiensis* (page 684). The age of these interesting relics is doubtful, but they are evidently Pleistocene.

In Asia.—Asia has given us in *Pithecanthropus* one of the oldest known relics of the Hominidæ, found at Trinil in the island of Java. The expeditions of the American Museum to Mongolia, under Dr. Andrews, have thus far found no fossil men; but they have found an abundance of artifacts of apparent Mousterian age (see page 678), and hence these so-called Dune Dwellers may have belonged to the Neanderthal species. Actual skulls of Neanderthal man were found, however, in caves near Tiberias on the Sea of Galilee. Both of these occurrences point to a far wider distribution of this type than was formerly known. Peking man, *Sinanthropus pekingensis*, a very primitive type, to judge from two isolated teeth, was discovered at Chow Kow Tien in 1921, and further exploration in 1928 has revealed jaws and skulls at this locality.

In Europe.—It is in Europe, however, that the tale of human prehistory is the most complete, not only through the happy accident of preserval, but because it has been much more thoroughly explored than has the Asiatic evolutionary center. Nevertheless, the latter holds the greatest hopes for future exploration since, as we have emphasized, Europe is too small to be an adaptive radiation center and European prehistoric men represent waves of migration from the greater continent.

The European record, however, has enabled us to name and define a number of distinct human species and here the record of the cultural evolution of man is also unusually complete. Hence European chronology is taken as a standard in describing discoveries from any portion of the world.

CULTURE CHRONOLOGY

Modified from MacCurdy

	Ice Age Chronology	Cultural Chronology			Human Species
Holocene (Recent)		Iron Age			
		Bronze Age			
	4 Post-Glacial	Neolithic		Campignian	
		Mesolithic		Maglemosean Azilian-Tardenoisian	*Homo sapiens*
QUATERNARY *Pleistocene*	IV Glacial (Würm)	*Paleolithic*	Upper	Magdalenian Solutrean Aurignacian	Crô-Magnon Man
	3 Interglacial (Riss-Würm)		Lower	Mousterian	*Homo neanderthalensis*
	III Glacial (Riss)			Acheulian	
	2 Interglacial (Mindel-Riss)				*Homo heidelbergensis* *Eoanthropus*
	II Glacial (Mindel)			Chellean	*Sinanthropus*
	1 Interglacial (Günz-Mindel)			Pre-Chellean	*Pithecanthropus*
	I Glacial (Günz)				
TERTIARY *Pliocene*		*Eolithic*		Foxhallian Ipswichian Cantalian (?)	

Pithecanthropus.—The Java ape-man, *Pithecanthropus erectus* (Fig. 255, and Pl. XXXI,A), was first discovered in Trinil, and elsewhere in central Java, in 1891. The type consists of a calvarium or skull cap, a left thigh bone, and two upper molar teeth. The skull, which has beetling brows or tori, appears relatively long and narrow, a characteristic of most prehistoric crania (except some of the latest), in contrast with those of the apes. In profile the calvarium is extremely low, the highest point

being at mid-length, while the rear part is heavy, implying a lack of that delicate balance characteristic of an entirely erect posture. This seems at variance with the evidence offered by the straight thigh bone, which caused the discoverer, Dr. Dubois, to give the specific name *P. erectus* to the form. But heavy neck muscles are indicated, which are correlated with a thrust-forward muzzle and generally bestial appearance. The cranium has been cleared of its contained matrix and a cast of the interior taken which shows the general form and proportions of the brain. While the exterior of the skull is like that of a gigantic gibbon, the brain was essentially human, but with a number of very primitive features. Two or three of these are in the areas which are the last to develop in the brain of a modern child, which throws an interesting side light on the stage of evolution of the *Pithecanthropus* brain.

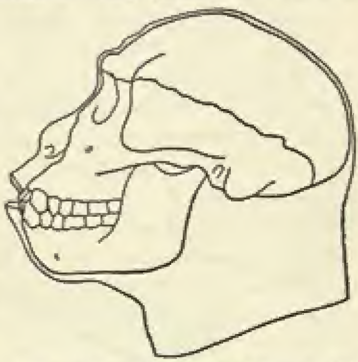

FIG. 255.—Restored head of Java ape-man (*Pithecanthropus erectus*). (After Lull, based upon McGregor.)

The cranial capacity has been estimated at 940 cubic centimeters, compared with 580 for a very large male gorilla and 1500 for an average European skull. But size is not the only thing, for the undeveloped portions are equally important, and the *Pithecanthropus* brain is deficient in the so-called prefrontal and parietal areas, the former particularly being the seat of the higher mental faculties. Broca's area, the seat of motor speech, and the auditory speech center are sufficiently developed to show that this primitive type possessed essentially human articulate speech, however rudimentary it may have been. The restoration of the face has been most carefully done and, while the evidence is far from complete, in all probability represents an approximation of the actual condition. It is based on the calvarium and the teeth and was checked by another very fragmentary specimen found twenty-four miles away.

Sir Arthur Keith estimates the height at 5 feet 8 inches, with a weight of 11 stone or 154 pounds, close to the average of modern man. Thus *Pithecanthropus* lies much nearer to man than the apes but is probably not in the direct line leading to modern man.

Peking Man.—*Sinanthropus pekingensis* is thus characterized: cranial walls very thick; tori huge, very low receding forehead, low cranial dome. Mandible chinless with massive canine teeth. Teeth large with both ape-like and human characters. Skeleton unknown, but evidence suggests an erect gait. *Sinanthropus* and *Pithecanthropus* may prove variants of the same human type.

Heidelberg Man.—*Homo heidelbergensis* (see Fig. 256), the Heidelberg man, represents one of the two oldest recorded European races, geologically speaking. The type was discovered in 1907 in river sands, 79 feet below the surface, at Mauer, near Heidelberg, South Germany. The relic consists of a perfect lower jaw with the dentition (see Fig. 257,C). This interesting relic shows a curious combination of characters, for, while the teeth are essentially human, the massive jaw is ape-like, so much so that, were the symphysis alone present, it might be taken for that of a gorilla-like form, while the rear ascending portion resembles a gibbon's, except for size. The chin slopes away as in the Piltdown man, while the area for muscular attachment is extremely powerful. The teeth, relatively small for the jaw, form a continuous series, and the canines do not rise above the level of the other teeth, both of which are human features in contrast with those of the apes. The teeth have short divergent roots, a bulging crown, and a relatively large pulp cavity, which Keith considers as an adaptation to a peculiar sort of diet. He compares the teeth to those of cattle, whose harsh vegetal food is obvious, hence he has coined the word taurodont (ox tooth) by way of a descriptive term. This is a characteristic, unape-like, found nowhere else among men other than in the Neanderthal race, to which Heidelberg man is supposed to be ancestral, and therefore seems to debar both from our own direct lineage.

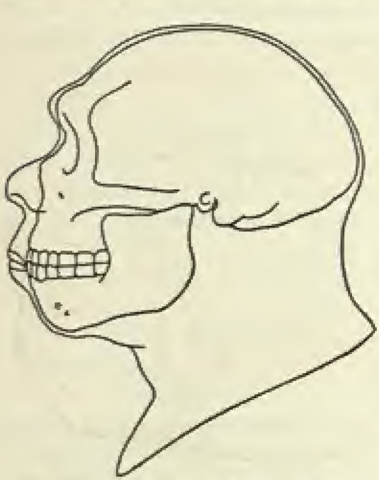

FIG. 256.—Restored head of Heidelberg man (*Homo heidelbergensis*). (After Lull, based upon McGregor.)

Recently other material has come to light in the Mauer sand pit, some of which may pertain to *Homo heidelbergensis*, but detailed descriptions are not yet available. The material seems, however, to bear out our conception of the brutal appearance of this ancient type.

Associated with the Heidelberg jaw is an extensive warm-climate fauna: straight-tusked elephant (*E. antiquus*), Etruscan rhinoceros, primitive horse, bison, wild cattle (urus), bear, lion, and so on, all of which aid in establishing the date of the jaw as Second Inter-glacial and its age, conservatively estimated, at from 300,000 to 375,000 years. The cultural evolution of Heidelberg man is indicated by the presence of eoliths, flint implements of the crudest workmanship, if indeed their apparent fashioning is not merely the result of use.

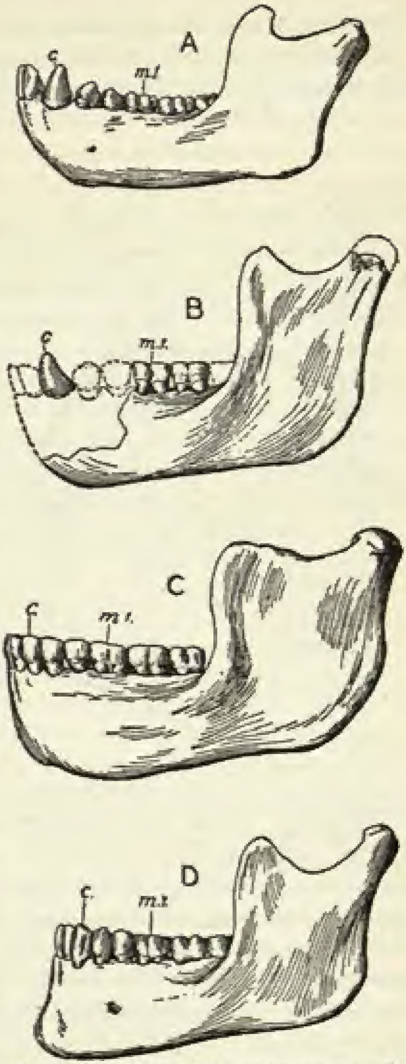

Fig. 257.—Jaws, left outer aspect, of A, chimpanzee, *Pan*, sp.; B, Piltdown man, *Eoanthropus dawsoni;* C, Heidelberg man, *Homo heidelbergensis;* D, modern man, *H. sapiens; c*, canine; *m 1*, first molar. (After Woodward.)

Neanderthal Man.—The specimen of Neanderthal type, *Homo neanderthalensis* or *primigenius* (Figs. 258, 259, 262, and Pl. XXXI, C), was discovered in 1856 not far from Düsseldorf in Rhenish Prussia. Here the valley of the Düssel forms the deep Neanderthal ravine, whose

limestone walls are penetrated by caverns, in one of which the remains were found. What was doubtless a perfect skeleton at the time of its discovery was so injured by its finders that only a portion of it, which was preserved in the Provincial Museum at Bonn, was saved. Previous to this, however, in 1848, a skull of this race had been found at Gibraltar, but its significance was not realized. Recently another skull has been found in Gibraltar.

The Neanderthal man, a prophet of an unknown race, was for a time utterly without honor though of course the subject of a most heated controversy, being considered as non-human, or as owing its distinctive characters to disease. The sagacity of Huxley threw true light upon the problem, though it was not until the mute testimony of other representatives of the race (the men of Spy) was offered that even Huxley's masterful conception of the Neanderthal characters was taken as an accepted fact. Professor Huxley's description of the Neanderthal type is classic. He says:

FIG. 258.—Restored head of Neanderthal man (*Homo neanderthalensis*). (After Lull, based upon McGregor, and Boule.)

"The anatomical characters of the skeletons bear out conclusions which are not flattering to the appearance of the owners. They were short of stature but powerfully built, with strong curiously curved thigh bones the lower ends of which are so fashioned that they must have walked with a bend at the knees. Their long depressed skulls had very strong brow-ridges; their lower jaws, of brutal depth and solidity, sloped away from the teeth downwards and backwards, in consequence of the absence of that especially characteristic feature of the higher type of man, the chin prominence."

Subsequently many more specimens have come to light, at Spy in Belgium, at Krapina in Croatia, at Le Moustier, La Chapelle-aux-Saints and La Ferrassie in France, and at Mt. Carmel near the Sea of Galilee. These, while differing in various details, effectually serve to establish the race, whose main characteristics

are: heavy, overhanging brows, retreating forehead, long upper lip; jaw less powerful than that of Heidelberg man but very thick and massive; chin generally strongly receding but in process of forming; dentition extraordinarily massive in the La Chapelle specimen, whereas in those of Spy the teeth are small. The skull in many characteristics is nearer to the anthropoids than to modern man.

The brain is large and its volume is surely human, but the proportions are again less like those of recent man than like the anthropoids. The chest is large and robust, the shoulders broad, and the hand large, but the fingers are relatively short, the thumb lacking the range of movement seen in modern man. The knee was somewhat bent, the leg powerful, with a short shin and clumsy foot, clearly not of cursorial adaptation. The posture is usually described as not fully erect, but Dr. McGregor says that it was slouching rather than stooping. The average stature was about 5 feet, with a range from 4 feet 8 inches to 5 feet 3 inches, partly sex differences. The body was stocky and powerful with loose-jointed limbs, so that the walk must have been an easy, shuffling gait. This, together with the huge head with the face thrust forward to accommodate the heavy jaw and the powerful neck muscles, gives an unlovely picture of this interesting type.

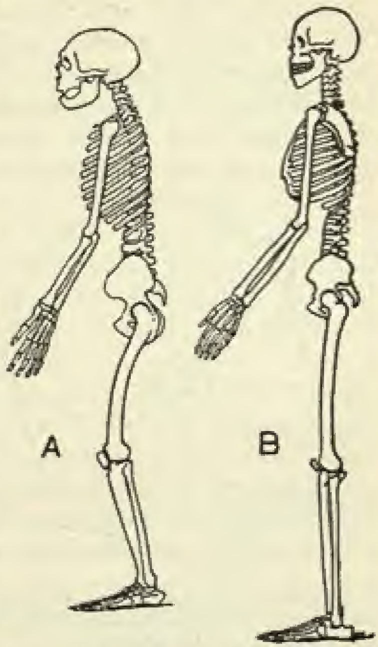

FIG. 259.—Skeleton of Neanderthal man; (A), *Homo neanderthalensis*, compared with that of a living native Australian; (B), *Homo sapiens*, the latter the lowest existing race. (After Woodward.)

The lower jaw is a derivative of that of Heidelberg, although lighter and with the rudiment of a chin, and the same taurodont specialization of the teeth is indicated. The brain is large but relatively simple in organization, especially in the primitive frontal lobes and Broca's area, implying not only limited intellec-

tual capacity but limited thought transmission as well. Culturally, Neanderthal man is classed as Mousterian, and the presence of a comparable industry in Mongolia (Dune Dwellers) and the Galilean skulls point to Asiatic distribution if not origin.

Neanderthal man lived in Europe from the Third Interglacial stage through the Fourth Glacial, a duration of thousands of years, and then became extinct, from twenty to twenty-five millenniums ago. He seems to have been an actual lineal successor of the man of Heidelberg, but was throughout his long career an unprogressive, static race. One of the most remarkable features in connection with this race, however, was the very reverent way in which the dead were buried, with an abundance of ornaments and finely worked flints. This can have but one interpretation, the awakening within this ancient type of the instinctive belief in spiritual immortality!

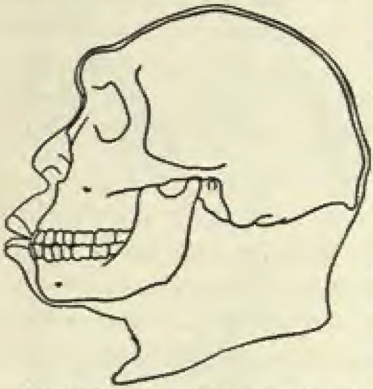

Fig. 260.—Restored head of Rhodesian man (*Homo rhodesiensis*). (After Lull, based upon Woodward.)

Rhodesian Man.—*Homo rhodesiensis* (see Fig. 260) was discovered in 1921 at Broken Hill in Northern Rhodesia. The remains consist of an almost perfect skull, lacking the lower jaw, together with portions of the limb bones and other skeletal elements. Fragments of a second individual were also found, sufficient to establish the race. Details of the cranium point to a number of simian characters, and the skull, in spite of certain specializations, is of a relatively low type. In the huge beetling brows, the flattened skull top, and other details it shows a strong resemblance to Neanderthal man, an undoubted relative. While the face, with its forwardly projecting jaws, is extremely brutal, the brain was large, 1300 cubic centimeters, somewhat less than any known Neanderthal except possibly the first Gibraltar skull, but again deficient in those regions last to be developed in ontogeny. There is a lack of harmony between the relative development of face and brain, as though Rhodesian man had not yet discarded the general utility of the mouth which preceded that of the hands, which in turn depends on brain power.

The teeth are entirely human, set in a finely arched palate and the third molars or wisdom teeth are somewhat smaller than are the others, a modern tendency found in but one other recorded instance among prehistoric men. There is, however, evidence of dental caries or tooth decay, together with other indications of disease in the skull, again an undesirable modern attribute, extremely rare in prehistory. The posture of this six-foot man was thought to be erect, but of this there is some doubt.

The dating of this interesting type is difficult. The skull is impregnated with mineral matter, as are the associated animal remains, and Bather thinks that, whatever the age of the latter, that of the skull is appreciably older. But the animals are all of the present African fauna which, however, has a distinct Pleistocene facies as compared with that of Asia. Rhodesian man is therefore of respectable antiquity, surely Pleistocene, although where he should be placed in the European chronology is not apparent.

The human species thus far discussed are all characterized by the huge brow ridges or tori, confluent above the nose, and by a low, flat forehead, inferred of course in the case of Heidelberg man. With the exception of *Pithecanthropus* and *Sinanthropus*, they all belong apparently to one *phylum*, the Neanderthalid, in spite of the immense time interval between Heidelberg and the true Neanderthal men.

Those yet to be discussed, Piltdown and Crô-Magnon men, lack the tori, and the forehead is steep. Otherwise they have little in common, and as a consequence their relationship is not clear.

Piltdown Man, *Eoanthropus dawsoni* (see Fig. 261, Pl. XXXI, B).—In 1912 was announced the discovery of a very ancient human relic from the Thames gravels at Piltdown, Sussex, England. When first discovered the skull was in large measure intact but was carelessly broken and thrown on the dump, to be painfully retrieved later. The single fragment saved by the workman was given to Mr. Charles Dawson, who, together with Sir Arthur Smith Woodward of the British Museum of Natural History, secured a number of additional portions, which were then laboriously reconstructed by the latter. As few of the pieces formed actual contacts with one another, the results of several attempts naturally varied slightly, especially as to cranial content, but the general form was clearly established. The parts consisted of parietal, temporal, and

a portion of the occipital bones, together with the nasals, a canine tooth, and part of the lower jaw containing several molars. It was not over the essential form of the skull but over the lower jaw that controversy arose, for this bone of contention had so many simian features that many felt it could not possibly belong with the skull, Gerrit Miller going so far as to pronounce the jaw that of an extinct chimpanzee, to which he gave the name *Pan vetus*, and the association purely accidental. Later opinion practically agrees that, in spite of its lack of harmony with the degree of evolution shown by the cranium, the jaw really may pertain to the same individual, and a second yet more incomplete individual bears out the belief that it is another instance of the evolutionary advance of cranium over face which we have seen in the case of Rhodesian man.

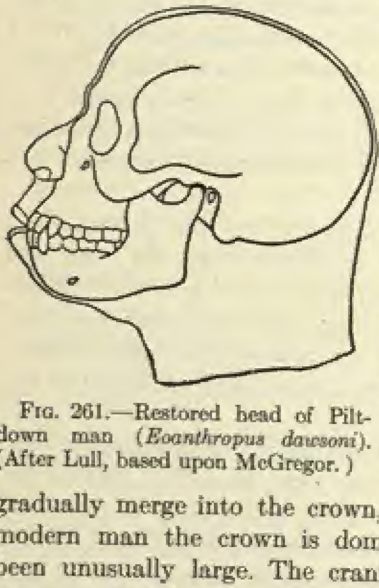

FIG. 261.—Restored head of Piltdown man (*Eoanthropus dawsoni*). (After Lull, based upon McGregor.)

The exterior of the skull, as now restored, is in no sense apelike, much less so in fact than the far later Neanderthal and Rhodesian men. The tori are lacking, and the forehead is steep, but the relative breadth of the rear portion and the inward slope of the sides, which gradually merge into the crown, do depart toward the ape; in modern man the crown is dome-shaped. The face must have been unusually large. The cranial walls are enormously thick, more so than in any other human skull, which makes the interior comparatively small, 1350 cubic centimeters, compared with 1500 for the average European. Eliot Smith sums up a description of the brain as the most primitive and ape-like human brain hitherto discovered, evidently excluding that of *Pithecanthropus*.

The jaw represents the imperfect right half. Enough remains to show a very retreating chin, but, while the molar teeth are human, the canine is not and must have interlocked with its opposite, as do those of the apes. Thus the jaws seem to have retained a large share of the general utility which goes with the

undeveloped brain. The associated flint implements are extremely crude, which is further evidence of the low estate of *Eoanthropus*. Chronologically Piltdown man is not surely dated. He was interglacial, the associated animal remains indicate that, but whether first or second is in question. He cannot be placed within our genus, *Homo*, since his peculiar morphology excludes him; rather has he been called *Eoanthropus*, the dawn man. *Eoanthropus* may also be barred from the direct ancestry of modern man.

Homo sapiens.—This Linnæan species includes all existing men, of whatever race, and some extinct men. They have a number of distinctive characters in common, although in varying degree. These are, first, the entirely erect posture, with four reversed curves in the spine which act as a shock-absorbing device to protect the nicely poised skull. The limbs are straight, but the segmental proportions vary racially and individually. The skull also varies in size and relative proportions, such as length to breadth. The forehead is generally steep, and the continuous brow ridge is absent. Thus there is ample space for the fullest mental development. The final distinctive feature is the jutting chin prominence, the result of the reduction of the dental arch. In the lower existing races, Australian and Negro, the teeth are fine and regular and are well spaced; in the higher races, on the other hand, they are apt to be crowded and out of alignment, due to further progressive reduction of the jaws.

Crô-Magnon Man.—The original finds of the men of the Crô-Magnon race (see Figs. 263, 264, Pl. XXXI, D), *Homo sapiens*, were made at Gower, Wales, and at Aurignac, France. In the latter place seventeen skeletons came to light in 1852, but were buried in the village cemetery and thus lost to science, and not until 1868, when five more skeletons were discovered in a rock shelter at Crô-Magnon, France, was the race established. These individuals, an old man, two young men, a woman and a child, are thus the type Crô-Magnons. This magnificent race is thus characterized:

Skull large but narrow, with a broad face, hence disharmonic. Facial angle equalling the highest type of *Homo sapiens*. Jaw thick and strong, with a narrow but very prominent chin. Forehead high and orbital ridges reduced. Brain not only of high type but very large, that of the women exceeding the average male brain of today.

The stature of the old man was 5 feet 11 inches; the average for males being 6 feet 1.5 inches,[1] for women 5 feet 5 inches, a great disparity. The lower segments of the limbs were long, in contrast with the Neanderthal type, hence the men of Crô-Magnon were swift-footed, while those of Neanderthal were slow. Osborn says:

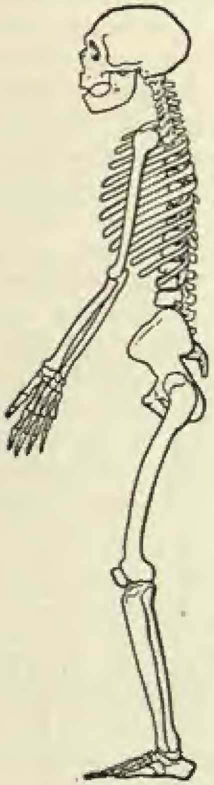

FIG. 262. — Skeleton of Neanderthal man, *Homo neanderthalensis.* (After Boule.) Compare with Fig. 263, which is drawn to the same scale.

"The wide, short face, the extremely prominent cheekbones, the spread of the palate and a tendency of the upper cutting teeth and incisors to project forward, and the narrow, pointed chin recall a facial type which is best seen to-day in tribes living in Asia to the north and to the south of the Himalayas. As regards their stature the Crô-Magnon race recall the Sikhs living to the south of the Himalayas. In the disharmonic proportions of the face, that is, the combination of broad cheekbones and narrow skull, they resemble the Eskimo. The sum of the Crô-Magnon characters is certainly Asiatic rather than African, whereas in the Grimaldis [of which specimens have been found in association with Crô-Magnons at the Grotte des Enfants, near Mentone] the sum of the characters is decidedly negroid or African."

The Crô-Magnons again show by their elaborate burial customs how old and well founded is the belief in life after death. They are undoubtedly the people who left in the caverns of France and Spain the marvellous examples of upper Paleolithic art so fully described by Abbé Breuil. They lived for a while contemporaneously with the men of Neanderthal and may have contributed somewhat to the final extinction of the latter. In the course of time, however, they too declined, although to this day survivors of the race may be seen in Dordogne, at Landes near the Garonne in Southern France, and at Lannion in Brittany.

[1] The tallest living races of men are the Highland Scots and the Patagonians whose height averages 5 feet 11 inches to 6 feet.

FIG. 263. — Skeleton of man of Crô-Magnon race, *H. sapiens*, from the Grotte des Enfants, near Mentone. (After Verneau.)

The decline of the Crô-Magnons, with their artistic culture, "may have been partly due to environmental causes and the abandonment of their vigorous nomadic mode of life, or it may be that they had reached the end of a long cycle of psychic development. . . . We know as a parallel that in the history of many civilized races a period of great artistic and industrial development may be followed by a period of stagnation and decline without any apparent environmental cause." (Osborn.)

Europe was repopulated after Crô-Magnon decline by later invaders from the Asiatic realm, the so-called Mediterranean narrow-headed and the Alpine broad-headed types, etc., probably differentiated in Asia in early Paleolithic times. The repopulation took place in the Upper Paleolithic. The origin of the Nordic race is in doubt.

Evidences of Human Antiquity

Great Variation.—These, briefly summarized, are, first, great variation. If man is monophyletic, that is, derived from a single prehuman species, there is little reason to believe otherwise, he must be old, for while the adaptations to ground-dwelling after the descent from the trees were doubtless relatively rapidly acquired, the differentiation into the various races due perhaps largely to climatic influences rather than to any notable environmental change, must have been slowly attained. As corroborative evidence we have but to point to the mural paintings on Egyptian monuments, dating back several thousand years, in which are depicted the Ethiopian, Caucasian and others, which

are in some instances striking likenesses of the present-day Egyptians.

Universal distribution is, in animals, another mark of antiquity; in man, it is probably less so because of his greater intelligence. And yet before transportation had become a science man's spread over land and sea was extremely slow.

High intelligence as compared with that of the anthropoids is also a mark of antiquity, for the brain, especially the type of brain found in the higher human races, must have been very slow of development. Our study of fossil man shows this.

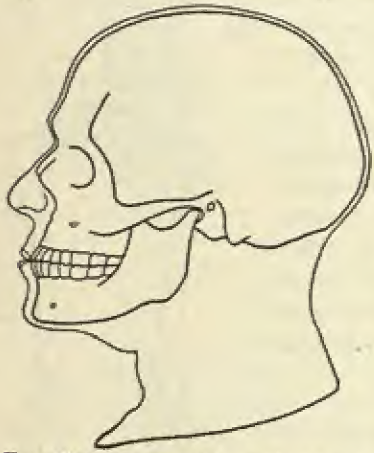

Fig. 264.—Restored head of Crô-Magnon man (*Homo sapiens*). (After Lull, adapted in part from McGregor.)

Communal life, division of labor and all of the complicated interactions which it brings about, and the development of law and religions all have taken time. When we realize that Babylonian texts, twice as remote as the patriarch Abraham, give evidence of highly perfect laws and of a civilization which must have antedated their production by centuries, we gain another yet more emphatic impression of human antiquity. Add to all this the paleontological evidence of man's association with various genera and numerous successive species of prehistoric animals of which he alone survives, and the evidence is complete.

Future of Humanity

Because of his intelligence, tool using, and communal life man is little subject to the laws which govern the adaptation of animals to their environment. The law of adaptive radiation, which, as we have seen, applies equally well to the insects, reptiles, and mammals, fails in its application to mankind; and yet man has become as thoroughly adapted to speed, flight, to the fossorial and aquatic as they; but his adaptation is artificial and to a very small extent affects only his physical frame, while theirs is

natural and the stamp of the environment is deeply impressed upon the organism.

Man's physical evolution has virtually ceased, but in so far as any change is being effected, it is largely retrogressive. Such changes are: reduction of hair and teeth, and of hand skill; and dulling of the senses of sight, smell, and hearing upon which active creatures depend so largely for safety. That sort of charity which fosters the physically, mentally, and morally feeble, and is thus contrary to the law of natural selection, must also in the long run have an adverse effect upon the race, unless offset by an enlightened eugenics.

Man is hardly as yet subject to Malthus' law, for while he is increasing more rapidly than any other mammal, owing largely to the care of the young which makes the expectation of life of the new-born relatively very high, his migratory ability, but above all his intelligence, save him from the application of the law. A single new discovery such as that of electricity may increase his food supply and other life necessities several fold. His future evolution, in so far as it is progressive, will be mental and spiritual rather than physical, and as such will be the logical conclusion of the marvellous results of organic evolution.

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EPILOGUE

THE PULSE OF LIFE

The stream of life flows so slowly that the imagination fails to grasp the immensity of time required for its passage, but like many another stream it pulses irregularly as it flows. There are times of quickening, the expression points of evolution, which are almost invariably coincident with some great geologic change, and the correspondence is so exact and so frequent that the laws of chance may not be invoked by way of explanation. The geologic changes and the pulse of life stand to each other in the relation of cause and effect. This statement does not, however, imply the acceptance of the Lamarckian factor any more than that of natural selection, for whether the influence of a changing environment acts directly upon the creature's body, or indirectly through induced habit, or, whether it merely sets a standard to which animals must conform if they would survive, matters not; the fundamental principle remains that changing environmental conditions stimulate the sluggish evolutionary stream to quickened movement.

Many of these pulsations have been described in the foregoing pages, and in each instance we have attempted to define the physical change which served to accelerate the flow of life. And in almost every successful attempt we have found the immediate influence to be one of climate, either of temperature or moisture variation, due sometimes to topographic, at others to general atmospheric conditions. Back of these climatic changes lies, as one of the great fundamental causes, earth shrinkage, with a consequent warping of the crust which produces mountain ranges and enlarges the lands. Thus it will be seen that the most momentous changes, so far as influence on life is concerned, may have, geologically speaking, a very simple basic cause.

In so far as we can recognize cause and effect, the record of the crises of evolution stands as follows:

For the origin of life itself there is no known geologic cause other than the gradually attained fitness of the earth to be the abode of organic beings. Nor do we surely know of any geologic event which

impelled the lime-secreting habit of animals and plants and thus made possible an adequate fossil record of their life. This habit was attained, however, by the animals in the Upper Cambrian, and much earlier by the water-living algæ among plants.

The origin of vertebrates, another event of high importance, occurred much earlier than mid-Ordovician time, for in rocks of that period are preserved fossils which indicate that chordate evolution was already well along upon its course, as the creatures recorded are highly specialized, armored offshoots of a primitive stock.

The main dynamic, and hence anatomic, distinction between vertebrates and invertebrates lies in the fact that the former are principally active motor types, while the latter, with some striking exceptions, such as the predaceous cephalopods, are sluggish non-motor organisms many of which are actually sedentary in their habits and adaptations. That this evolutionary distinction is largely the result of habitat seems evident, the vertebrates being a response to dynamic waters, the invertebrates to static. The origin of vertebrates, therefore, apparently implies no more than quickened rivers and inhabitants of right potentiality; it could not, in all probability, have occurred either in the sea or in land waters borne upon a flat topography. Hence we should look for a great diastrophic movement or elevation of the lands such as would accelerate the flow of terrestrial rivers, for in all probability a potent stock, possibly worm-like forms, had peopled the sluggish waters for a long period antecedent to the actual change. Several such movements are recorded during pre-Cambrian time; but that of the interval between the Proterozoic and the Cambrian (see Fig. 265), seems to fill the time requirements best of all, as the others are immeasurably remote.

Another event of immense importance to future evolution was the emergence of the vertebrates from their limiting aquatic environment. That this emergence was by way of the strand from sea to land seems hardly probable, for no phylum of animals has ever chosen this readily available route. Isolated genera or even species which collectively form rare exceptions to the mode of living of their allies have traversed this road, but there is not sufficient stimulus to produce a notable migration. The vertebrate emergence was from the rivers to the lands, and the impelling cause the increasing aridity consequent upon the Silurian uplift. This re-

duced the abundant rivers to sluggish streams and finally to residual bodies of water, imperfectly oxygenated, which placed a premium on lung-breathing on the part of the contained fishes. When the final dwindling of their habitat left them stranded, such as could become exclusively air-breathing survived, giving rise to the amphibia, but those which could not, perished, except that in some remote asylums where a vestige of their habitat persisted, the lung-fishes also survived, for their descendants, few as to kinds, are still extant.

With the recurring moisture of the Coal Measures, amphibia throve and multiplied, returning to the ancestral waters seasonally to bring forth their young, but toward the latter part of the Mississippian period increasing aridity and reduction of temperature are again manifest, making this annual return less readily possible and stimulating the evolution of the exclusively air-breathing reptiles.

In the Permian recurs the same chain of events—continental rise, increased aridity, and, this time, glaciation, especially in the southern hemisphere. The following Triassic period was likewise a time of aridity, amelioration of climate coming after its close. Reptiles being already established, the climatic conditions stimulated an event in the evolution of terrestrial animals second in importance only to their emergence: the origin of mammals. Aridity paved the way by developing active types among the reptiles, and this was apparently a necessary antecedent to the establishment of warm blood, through quickened metabolism and raising of the body off the ground. Increasing cold then placed a premium on ability to maintain this activity beyond the limits of the shortening summers, and this could only come about through the acquiring of a constantly maintained temperature, in other words, of warm blood. Out of one reptilian stock were to rise the warm-blooded quadrupedal mammals, and out of another the warm-blooded bipedal birds. The former, however, were kept so effectually in check during the Mesozoic, apparently by the dominant reptiles, that their known evolution amounts to comparatively little until Eocene time.

Aridity in the Triassic, necessitating swiftness of motion, may have caused the rise of the bipedal dinosaurs, just as aridity and bipedality among modern lizards are the result of similar association of cause and effect.

Climatic oscillation, giving rise to humid conditions during the

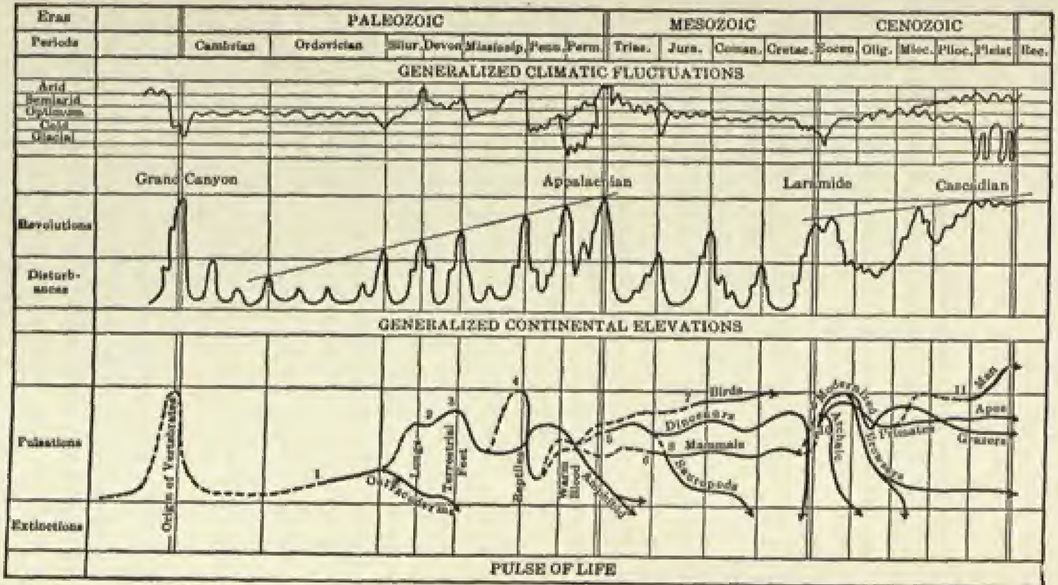

FIG. 265.—Diagram of the pulse of life. Climatic line: minor jogs merely indicate climatic oscillations; doubling of lines, climatic zones where aridity and cold are differentiated; single line, uniformity of conditions the world over. Continental elevation line: up-slopes mean rising diastrophism; down-slopes, periods of erosion before continents are low enough to have mantles of sediment spread upon them, *i. e.* the intervals. Whole Cenozoic has about the time valuation of the Permian. First records on the life line: 1, vertebrates; 2, lung-fishes; 3, footprint; 4, reptile; 5, dinosaur; 6, mammal; 7, bird; 8, sauropod dinosaur; 9, archaic mammal; 10, modernized mammal; 11, man. (After Lull. Courtesy of the Yale University Press.)

Jurassic, furnished an amphibious habitat which tempted the increasingly large saurischian dinosaurs to forsake their ancient dwelling-places and abandon the strenuous life of a carnivore for the slothful ease of an amphibious herbivore, and their restriction in the early Cretaceous may have been due in part at least to a dwindling of their habitat.

The cause of dinosaurian extinction at the close of the Mesozoic is yet unknown, but the fact that it was coeval with the world-wide Laramide Revolution, which must have given rise to a far-reaching chain of results, gives evidence that here we have again a basic geologic cause.

It cannot be doubted that the cause or causes of dinosaurian extinction were an indirect stimulus to the first great deployment of the archaic mammals after their age-long suppression during the Mesozoic.

The archaic mammals in turn met their fate largely through the competition induced by the incursion of the modernized orders, and this again had for its prime cause the decreasing temperature in the north, which drove the modernized hordes from their ancient radiation centers along the several continental radii to the south. It is not without the realm of possibility that the somewhat severer and more variable climatic conditions of their northern home stimulated the modernized mammals to higher evolutionary attainment than did the more equable habitat of the archaic forms.

Increasing aridity during the Oligocene and Miocene, due again to continental uplift, gave great impetus to the grasses, which now became the dominant flora of the temperate realms. The effect of this on mammalian life was far-reaching for it caused the restriction and extinction of many browsing types and a wonderful deployment of the grazing forms—horses, camels, deer, and antelopes—which are so important a part of the earth's mammalian fauna to-day.

Finally, we have with the increasing elevation of late Miocene and Pliocene time, especially in central Asia, the culmination of the evolution of the various races of mammals which man has adopted as his fellow-workers—the domestic animals. And not only were the wolves and cats, the cattle, buffalo, sheep, and goats, the horses and camels, and all the host of the friends of man here finally evolved, but man himself, as a response to the same series of geologic changes by which the others were brought to their final frui-

tion. For variation in amount of moisture and increased cold in the north land, with the consequent restriction of tropical forests, brought the primates south, and still further cold and aridity reduced to residual tree-clad areas the forests within which dwelt the pre-human. These areas were finally destroyed, or at any rate so changed in their old tropical prodigality that the human precursor, as a means of preservation, descended from the trees and became man.

Increasing severity of climate during the periods of glacial advance had a profound influence upon primæval man, necessitating clothing and a search for and adaptation to diverse sorts of food. Man thus became in a large measure independent of climate and this was his first conquest of the forces of nature, a conquest which has led to others, so that now he has not only become the dominant form of animate creation, but has subjected to his will many of the very forces which through long ages have stimulated his evolution.

Thus time has wrought great changes in earth and sea, and these changes, acting directly or through climate, have always found somewhere in the unending chain of living beings certain groups whose plasticity permitted their adaptation to the newly arising conditions. The great heart of nature beats, its throbbing stimulates the pulse of life, and not until that heart is stilled forever will the rhythmic tide of evolution cease to flow.

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